The carbon dynamics and phenology of oak woodland growing in south-east England

Matthew Wilkinson

BSc, MSc

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Abstract

The following commentary presents original scientific research and peer reviewed publications submitted for evaluation for the award of PhD by Publication. The central theme for these publications is 'temperate forest functioning in a changing climate'. Papers are presented on forest carbon dynamics including the impacts of forest management and on forest phenology. The first two papers focussed on quantifying the carbon fluxes of a deciduous oak plantation. The paper: "Inter-annual variation of carbon uptake by a plantation oak woodland in south-eastern England" explored the effects of environmental and other biotic impacts on carbon uptake of an oak woodland. The second paper: "Effects of management thinning on CO_2 exchange by a plantation oak woodland in south-eastern England" investigated the impacts of disturbance following a management intervention. Maintaining the theme of 'temperate forest functioning in a changing climate', the next two papers focused on assessing the impacts of climate change on forests through alterations in their phenology. Paper three: "Variation in the date of budburst in *Quercus robur* and *Q. petraea* across a range of provenances grown in Southern England" assessed differences in the timing of budburst across 23 different European oak provenances all growing at the same site. Paper four: "Can upward-facing digital camera images be used for remote monitoring of forest phenology?" investigated the suitability of ground-based digital cameras for the automatic monitoring of forest phenology and developed methods to improve phenology quantification.

In combination with the 12 papers that I have co-authored and four recent conference presentations that I have delivered, this series of papers documents the original scientific research that I have carried out over the past 18 years and provides a narrative on this research. The thesis concludes with a set of future research recommendations that have developed from these studies.

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Finally, sincere thanks to all of my family for their support over the years, particularly my amazing wife Becky and my fantastic boys Joe and Sam who have supported me through every stage.

Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

Signature:

Contents

Chapter 1 - Introduction

1.1 Background

International attempts to limit greenhouse gas (GHG) concentrations, aimed at stabilizing human induced climate change, require a detailed understanding of the current and potential future role of forests to sequester and emit carbon. At the global scale, forests are estimated to sequester 2.4 ± 0.4 Pg C y^{-1} with temperate forests contributing 0.7 ± 0.09 Pg C y^{-1} (Pan et al., 2011) to this total. Forests, therefore, have an important role in the global carbon cycle and climate regulation as well as providing many other ecosystem services valued by society. However, this large global carbon sink is at risk. Direct human activities such as tropical land-use change, where forests are cleared for agriculture and timber, result in net carbon releases (Quéré et al., 2018). Furthermore, climate change is already having, and will continue to have, major consequences for our global forests. In the UK, the average temperature over the recent past (2008-2017) has been 0.8 °C warmer than the 1961-1990 average (UKCP18). Climate change projections indicate that, by the end of the 21st century, all areas of the UK are likely to be even warmer, with a greater degree of warming projected for summers than winters. Based on a high emission scenario, UK average warming (10%-90% probability levels) is projected to be in the region of 0.9 °C to 5.4 °C warmer in summers, and 0.7 °C to 4.2 °C warmer in winters by 2070 (UKCP18). Precipitation patterns are also likely to change, winters are likely to become wetter, whilst summers are projected to become drier. In addition, the frequency and intensity of extreme weather events is also likely to increase. Such changes in climate are likely to have major impacts on UK forests (UK CCC, 2017), yet there are still large uncertainties about how forests may respond to these climatic changes and the implications for subsequent biophysical and ecological interactions.

Forest Research (FR) is the research agency of the Forestry Commission (FC) and has been conducting scientific services to the UK forestry sector for over 60 years. Since the early 1990s, one of FR's main research programmes has been to improve understanding of: the possible impact of climate change on forests and woodlands; the role that forestry can have in mitigating GHG emissions; and how the forestry sector can adapt to a changing climate. The work presented in this thesis has originated from and contributed to this research programme.

In the UK woodland area is currently estimated to cover 3.17 million hectares which represents 13% of the total land area (Forestry Commission, 2018). This woodland area is estimated to contain a total carbon stock of 1.03 Pg C with approximately 72% of this stored in soils. The total annual net carbon sequestration rate of the UK's woodland is estimated at 5.73 Tg C y^{-1} (Forestry Commission, 2018) although due to relatively low planting rates of new woodland over recent years, this figure is projected to fall by 2030 to around 5.18 Tg C y^{-1} (Forestry

Commission, 2018). In England, broadleaved species make up around 74% of the woodland area, with oak (*Quercus* spp.) being the most commonly occurring species followed by ash (*Fraxinus excelsior* L.) and birch (*Betula* spp.) (Forestry Commission, 2018).

1.2 Methodological approaches

This thesis cites, in addition to others, four peer-reviewed journal articles that I have authored with a central theme of 'temperate forests functioning in a changing climate'. The papers address specific aspects related to both mitigation of GHG emissions and climate change impacts. Consideration is given to the causes of inter-annual variation in carbon fluxes, the effects of management and the climate control of phenology of an oak forest in the south of England. The full text of these manuscripts is included as separate chapters and will be referred to throughout this thesis. The main study site for these articles was the Straits Inclosure, Alice Holt Forest (51°07'N, 0°51'W). The Straits Inclosure is a 90-hectare block of oak-dominated woodland located on the Hampshire/Surrey border in the south of England and has been the focus of intensive monitoring and scientific research for more than 25 years (Monteith et al., 2016). In addition to the carbon flux research programme established in 1998, the Straits Inclosure is a Level-II observation plot, part of the European network (ICP Forests) programme (http://icp-forests.net) and a UK Environmental Change Network (ECN) site (http://www.ecn.ac.uk).

A combined approach using long-term forest monitoring techniques such as Eddy Covariance (EC), meteorological and camera observations, and short-term measurement campaigns such as soil CO_2 flux chamber measurements have been used for the primary data collection. A variety of statistical techniques such as partial least squares regression (PLS) and modelling approaches have also been used to analyse and interpret the results from these multi-annual measurements. These whole forest studies are not based on statistically replicated manipulation experiments, where a control and treatments are applied according to prescriptive protocols and strict statistical designs. Large scale experimental manipulation type studies are logistically difficult and potentially extremely expensive to carry out within mature forests, especially where the treatments involve climate manipulations (e.g. experimental warming, throughfall exclusion) or CO_2 fumigation (e.g. Free Air Carbon Enrichment). Furthermore, mature deciduous woodlands, characteristic of southern England, are typically small and inherently heterogeneous, for instance, they may comprise of different tree species or be planted on contrasting soil types. The approach adopted was, therefore, to collect and analyse the results of long-term forest monitoring research and to examine trends and anomalies in the carbon balance (over twenty years) and phenology (over eight years). Although this approach may have some disadvantages over the classic experimental approach (e.g. the length of time required), it allows forests to be observed in their 'natural'

state and provides a better insight into the response of mature ecosystems to long-term environmental changes such as variation in climate.

1.3 Areas of improved understanding

The original research presented in this thesis provides evidence, analysis and discussion aimed at improving our understanding on the components of, and the environmental controls on the carbon balance of a temperate deciduous woodland, and on how management thinning affected it. Specifically, the magnitude and long-term inter-annual variability in carbon sequestration rates of an oak woodland characteristic of the South of England have been quantified. This research has helped improve our understanding on the impacts of disturbances including management and other biological events (such as the damage caused by insects and disease) on forest carbon balances as well as on the climatic controls of budburst in oak trees. This research has also contributed to improved understanding on the interaction between climate and temperate tree provenances on the timing of budburst. Finally, this work has made a technical contribution to the methodology of camera-based phenology observations, demonstrating that ground-based camera systems can be used as a viable alternative to the more expensive usual tower-based systems.

Chapter 2 - Inter-annual variation of carbon uptake by a plantation oak woodland in south-eastern England

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Biogeosciences

Inter-annual variation of carbon uptake by a plantation oak woodland in south-eastern England

M. Wilkinson[1], **E. L. Eaton**[1], **M. S. J. Broadmeadow**[2], **and J. I. L. Morison**[1]

[1]Forest Research, Centre for Forestry and Climate Change, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK
[2]Forestry Commission, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

Correspondence to: M. Wilkinson (matthew.wilkinson@forestry.gsi.gov.uk)

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Abstract. The carbon balance of an 80-yr-old deciduous oak plantation in the temperate oceanic climate of the south-east of Great Britain was measured by eddy covariance over 12 yr (1999–2010). The mean annual net ecosystem productivity (NEP) was $486\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (95 % CI of $\pm 73\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), and this was partitioned into a gross primary productivity (GPP) of $2034 \pm 145\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, over a 165 ($\pm$ 6) day growing season, and an annual loss of carbon through respiration and decomposition (ecosystem respiration, R_{eco}) of $1548 \pm 122\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Although the maximum variation of NEP between years was large ($333\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), the ratio of R_{eco}/GPP remained relatively constant (0.76 ± 0.02 CI). Some anomalies in the annual patterns of the carbon balance could be linked to particular weather events, such as low summer solar radiation and low soil moisture content (values below 30 % by volume). The European-wide heat wave and drought of 2003 did not reduce the NEP of this woodland because of good water supply from the surface-water gley soil. The inter-annual variation in estimated intercepted radiation only accounted for ~ 47 % of the variation in GPP, although a significant relationship ($p < 0.001$) was found between peak leaf area index and annual GPP, which modified the efficiency with which incident radiation was used in net CO_2 uptake. Whilst the spring start and late autumn end of the net CO_2 uptake period varied substantially (range of 24 and 27 days respectively), annual GPP was not related to growing season length. Severe outbreaks of defoliating moth caterpillars, mostly *Tortrix viridana* L. and *Operophtera brumata* L., caused considerable damage to the forest canopy in 2009 and 2010, resulting in reduced GPP in these two years. Inter-annual variation in the sensitivity of R_{eco} to temperature was found to be strongly related to summer soil moisture content. The eddy covariance estimates of NEP closely matched mensuration-based estimates, demonstrating that this forest was a substantial sink of carbon over the 12-yr measurement period.

1 Introduction

Many terrestrial ecosystems, including forests, are sinks for carbon (C) (Unger et al., 2009), and globally between 1990 and 2007 forests were estimated to have a net sequestration of $1.1 \pm 0.8\,\mathrm{Pg\,C\,yr^{-1}}$ (Pan et al., 2011), equivalent to one-seventh of emissions from fossil fuel combustion and cement production (Reich, 2011). Forests therefore have a fundamental role in helping to regulate atmospheric CO_2 concentrations, and an improved understanding of the underlying processes is needed to inform the development of climate change mitigation strategies (Nabuurs et al., 2007). In the medium to long term, a growing forest stand will be a net carbon sink, but at shorter timescales and as they react to unfavourable weather conditions, they can also act as a source (Valentini et al., 2000). For example, the severe drought and extreme high temperatures experienced in Europe over the summer of 2003 led to an estimated net release from the continent's forests of $0.5\,\mathrm{Pg\,C\,yr^{-1}}$ (Ciais et al., 2005). Forest disturbance, changes in local climate or in phenology may also lead to a long-term forest carbon sink temporarily becoming a carbon source (Powell et al., 2006; Pereira et al., 2007; Noormets et al., 2008).

While forest mensuration methods are well suited to quantifying the long-term growth of forest stands (e.g. at 5 yr intervals), the infrequency with which measurements are

usually made means that they are unable to give reliable information about inter-annual variation in growth rates. Furthermore, as mensuration methods typically show only the net effect on the tree components, they do not give information about the C balance of whole ecosystems or about the effects of disturbance and recovery. Networks of long-term, continuous, direct measurements of CO_2 fluxes using the eddy covariance method have become a powerful tool in improving the understanding of C exchange between forests and the atmosphere (Baldocchi et al., 2001), and provide valuable information relating to their daily and seasonal changes and about the impact of management. Our understanding of the size of sink and extent of inter-annual variation is increasing as data from eddy covariance studies in forests in excess of 10 yr duration become available (e.g. Ito et al., 2005; Dunn et al., 2007; Ilvesniemi et al., 2009). Key aspects now being revealed include the following: impacts of climate change (Urbanski et al., 2007); the role of weather anomalies (Saigusa et al., 2008; Teklemariam et al., 2009); effects of pests and diseases (Allard et al., 2008) and the role of management (Saunders et al., 2012).

In this paper we present the results from 12 yr (1999–2010) of eddy covariance measurements of CO_2 flux above an 80-yr-old lowland oak woodland in a mild, temperate, oceanic climate in south-eastern England. The annual sums of net ecosystem productivity (NEP) and its component assimilatory (gross primary productivity, GPP) and respiratory fluxes (ecosystem respiration, R_{eco}) are given. The paper also examines the causes of inter-annual variability of the partitioned fluxes, and assesses the relationship with key climatic and biotic drivers.

2 Materials and instrumentation

2.1 Site description

The site is located in the Straits Inclosure, Alice Holt Research Forest, UK (51°07′ N, 0°51′ W), close to the Alice Holt Research Station in south-eastern England (Fig. 1). The site is affiliated with the FLUXNET network and is also included in several other monitoring and research projects: it is a Level-II observation plot of the European network (ICP Forests) programme (http://icp-forests.net) and a UK Environmental Change Network (ECN) site (http://www.ecn.ac.uk). The inclosure is a flat area with an elevation of 80 m; the surrounding landscape consists of mixed lowland woodland and both arable and pasture agricultural land. The site is managed by Forest Research, the research agency of the British Government's Forestry Commission.

Early maps and records show that the western half of the Straits Inclosure was wooded in 1787, with the eastern part under agricultural management. The whole 90-ha inclosure was planted in the 1820s with oak (Schlich, 1905)

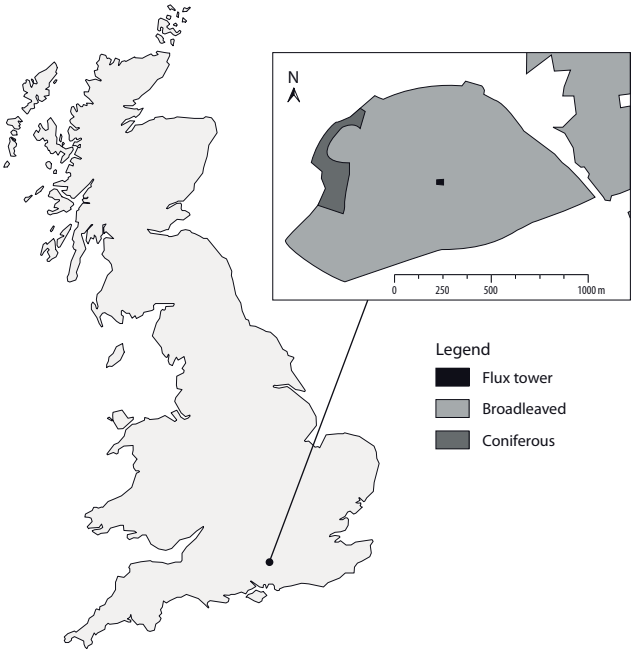

Fig. 1. Map of Great Britain with inset figure showing the location and layout of the Straits Inclosure.

and then replanted in the 1930s so that it is now a relatively homogeneous forest block managed as a commercial lowland oak forest. The main tree species is *Quercus robur* L., but other species, including European ash (*Fraxinus excelsior* L.), *Q. petraea* (Mattuschka) Liebl. and *Q. cerris* L., are present. There is a small area of mixed conifers consisting of Corsican pine (*Pinus nigra* subsp. *laricio* Maire.) and Scots pine (*Pinus sylvestris* L.) at the north-west edge of the woodland, and isolated pockets of Japanese red cedar (*Cryptomeria japonica* (L.f.) D. Don) are also present in the eastern area. The understorey is dominated by hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* Jacq.; Pitman and Broadmeadow, 2001). The soil is a surface-water gley (Pyatt, 1982), with a depth of 80 cm to the C horizon of the Cretaceous clay. Soil pH is 4.6 and 4.8 in the organic and mineral horizons respectively, and the soil organic C stock measured in the top 30 cm in 2004 was 87 t C ha^{-1} (Benham et al., 2012), and to 1 m depth in 1997 was 157 t C ha^{-1} (Table 3.7; Morison et al., 2012). Periodic tree measurements have been carried out at seven vegetation sampling plots as part of the ECN monitoring programme (Table 1). In addition, 18 forest mensuration plots (8 m in radius) were established in the western half of the inclosure during 2009; a density of 450 canopy trees per hectare was recorded, with a basal area of 29.7 m^2. In the recent past, different parts of the site have been thinned in 1991, 1995, 2000 and 2007.

Eddy covariance measurements of CO_2, sensible heat and water vapour flux were carried out at 28 m above ground level on a free-standing 26-m-high square-section mast (Gigalite 4, Litestructures Ltd, Pontefract, UK) located near to

Table 1. Mean annual biometric mensuration data for understorey and canopy tree species at the Straits Inclosure, Alice Holt Forest, for the period 1994–2011.

Year	Shrubs			Canopy Trees	
	Crataegus monogyna	*Corylus avellana*	*Ilex aquifolium*	*Fraxinus excelsior*	*Quercus robur*
Height (m)					
1994	3.5	6.8	Na	17.8	16.1
2002	3.9	7.4	5.4	19.9	19.6
2011	7.4	6.2	8.6	21.6	21.1
Diameter (cm)					
1994	6.0	6.4	Na	20.8	22.5
2002	4.6	6.0	7.5	23.9	28.6
2011	7.3	4.9	11.6	26.5	29.6

Na = not available

the centre of the inclosure (Fig. 1) providing a fetch over the woodland of 500 m, 700 m, 350 m and 600 m to the N, E, S and W respectively. Additional measurements of climatic variables were recorded from the mast or from the ground nearby (see below). The long-term mean (1971–2000) screen annual air temperature was 9.6°C and the mean annual precipitation 779 mm at the UK Meteorological Office affiliated weather station, Alice Holt, Farnham (51°10′ N, 0°51′ W), approximately 1.8 km from the measurement site.

2.2 Instrumentation

Half-hourly fluxes of energy (sensible and latent heat), momentum, CO_2 and water vapour have been measured continuously using the eddy covariance technique (Moncrieff et al., 1997) since 1998. The system is comprised of a three-dimensional sonic anemometer (model Solent R2, Gill Instruments, Lymington, UK) measuring wind vector components and a closed-path infrared CO_2 and H_2O analyser (IRGA, model LI-6262 until October 2005, LI-7000 thereafter, LI-COR Inc., Lincoln, NE USA) measuring atmospheric CO_2 and H_2O concentrations. Pure nitrogen was used as the zero CO_2 concentration gas flowing through the IRGA reference cell. Sample air was drawn from the inlet port at a point close to the sonic anemometer (horizontal separation of $\sim$ 10 cm) using a sample tube (Dekabon Ltd., Glasgow, UK) with an internal diameter of 6.15 mm, through two inline 1 micron PTFE Teflon filters (Gelman Acro 50) at a rate of 5.5 L min^{-1} by a small pump (Capex V2 SE, Charles Austen Pumps, Byfleet, Surrey, UK). Calibration of the IRGA using a reference standard gas was performed weekly. The raw high frequency data (20.8 Hz) were logged using the EdiSol software (Moncrieff et al., 1997), and for this study were available from 1 January 1999 through to 31 December 2010. The system was powered by battery, charged by solar panels and wind turbines until 31 May 2005, when mains power was installed, resulting in significant improvements to data collection.

Supporting environmental measurements recorded at the site included the following: wind speed and direction (model WA15, Vaisala, Helsinki, Finland), wet and dry bulb air temperature (model DTS-5, ELE International, Loveland, USA), above and below canopy solar radiation (tube solarimeters, Delta-T Devices, Cambridge, UK), global solar radiation (model CM2, Kipp & Zonen B.V., Delft, Netherlands), net radiation (model DRN-301, ELE International, Loveland, USA), soil heat flux (model HFP01, Campbell Scientific Ltd, Loughborough, UK), soil temperature at 10 cm depth (2K Thermistor, Delta-T Devices) and soil moisture (model ThetaProbe ML2, Delta-T Devices). All measurements were logged at 10 s intervals, and half-hourly averages recorded using data loggers (DT 500, dataTaker, Thermo Fisher Scientific, Australia).

Leaf area index (LAI) was assessed using litterfall traps located within the Level-II forest-intensive monitoring plot approximately 450 m from the flux tower. Canopy litterfall (leaves, twigs, frass, acorns, etc.) was collected in 10 cone-shaped traps held above the ground vegetation at height of 1.5 m, each with a collecting surface area of 0.33 m^2, and distributed randomly within the monitoring plot. Small cloth bags attached to the traps were collected every two weeks during the summer and autumn and subsequently sorted into their constituents. Leaf surface area was measured using a leaf area meter (model MK2, Delta-T Devices), and peak leaf areas back-calculated from cumulative litterfall (ICP Forests, 2004). Although the forest intensive monitoring plot has been subjected to a slightly different management regime than other areas of the forest, a comparison with litterfall traps from the area surrounding the mast (data not shown) indicates that the LAI values derived here give a good representation of the relative change in canopy density between years.

2.3 Calculation of CO_2 fluxes

The raw eddy covariance data files were re-processed with the Edinburgh University micrometeorological software tool EdiRe (http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe) following the basic procedures used in the CarboEurope project (Aubinet et al., 2000). Two-angle velocity signal coordinate rotation was applied to ensure that the vertical velocity signal was orthogonal to the plane of mean air flow. The lag time of the sample from the intake point to the cell of the closed-path analyser was determined by maximising the covariance between the vertical wind velocity and scalar concentration. Virtual temperature derived from the speed of sound was corrected for water vapour (Hignett, 1992). In order to account for flux loss caused by signal damping inside the tube, limited time response and sensor separation, etc, the usual spectral corrections were applied (Moore, 1986; Leuning and Moncrieff, 1990; Lenschow and Raupach, 1991; Massman, 1991) to

compute the corrected CO_2 and water vapour fluxes. In addition, an angle of attack correction was applied to correct for sonic anemometer velocity calibration errors at large ($> \pm 40$ degrees) angles of attack (Van der Molen et al., 2004).

Half-hourly net ecosystem exchange (NEE, $\mu mol\,m^{-2}\,s^{-1}$) was calculated using the corrected CO_2 flux, F_c as $NEE = F_c + S_c$, where $F_c = \overline{w'c'}$ is the covariance between the vertical wind velocity and the atmospheric CO_2 concentration, and Sc the rate of change in CO_2 storage per unit ground area in the air column below the eddy covariance IRGA intake. The storage term was estimated by the simple approach using only the change in CO_2 concentration measured at 28 m (Hollinger et al., 1994; Greco and Baldocchi, 1996):

$$S_c = \frac{\Delta c(z)}{\Delta t}\Delta z, \quad (1)$$

where $\Delta c(z)$ is the change in CO_2 molar density at height z, Δt the time period (30 min) and Δz the height of the eddy covariance sensor above ground (28 m).

After calculation of corrected NEE, and manual filtering of data for instrument failures and system maintenance, data filters were applied in order to remove extreme spikes, which were assumed to be not biologically valid data, an approach similar to that proposed by Papale et al. (2006) and Thomas et al. (2011). For each calendar year, NEE data were firstly split into either positive or negative values. Positive values greater than the mean positive value for the whole year plus three standard deviations were removed and the same approach applied to all negative values. A secondary stage data filter was then applied, removing positive values that were greater than the mean monthly value for that half-hourly period plus three standard deviations, and negative values less than the mean monthly value minus three deviations. Despiking filters were also applied to the latent heat flux (< -100 or $> 400\,W\,m^{-2}$) and to the sensible heat flux (< -500 or $> 500\,W\,m^{-2}$) NEE data when either of these criteria occurred were also removed.

A flux footprint probability analysis was carried out using the "footprint" calculation tool within EdiRe, which applies the model of Kormann and Meixner (2001) to a user-specified fetch. On average 65 % of the daytime flux originated within ~ 450 m of the tower, but at night this increased to ~ 600 m. Therefore, it is likely that a majority of the daytime flux originated from within the oak forest, particularly as the longest possible target fetch extends to over 800 m towards to the south-west of the tower, which is also the predominant (24.6 %) wind direction. However, we cannot exclude the possibility that fluxes were influenced by the adjoining agricultural land, especially when nighttime conditions were combined with southerly wind directions.

2.4 Gap filling

In order to create the continuous flux dataset required for carbon budgeting, and as an input for the partitioning of CO_2 fluxes, it was necessary to replace the missing and deleted values with appropriate values ("gap-filling"). The marginal distribution sampling (MDS) method described in Reichstein et al. (2005) and accessed through the on-line CarboEurope gap filling tool was used (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php). Whilst similar to the lookup table method (Falge et al., 2001), this approach also considers the temporal auto-correlation of the fluxes, replacing missing data with an average value under similar meteorological conditions. This method was chosen because it is widely accepted and has been employed by both CarboEurope and FLUXNET (Moffat et al., 2007; Papale et al., 2006). Half-hourly NEE values were screened against a friction velocity (u^*) threshold using the method described by Reichstein et al. (2005) and implemented through the on-line gap filling tool. The dataset is split into six temperature categories of equal sample size and then further subdivided into 20 classes based on u^* values. The u^* threshold for each temperature class is calculated as the u^* class where the nighttime flux reaches more than 95 % of the average flux within the higher u^* classes. The final threshold is defined as the median of the thresholds, and this procedure is applied to the subsets of four 3-month periods to account for seasonal variation of vegetation structure. The mean u^* threshold for the period 1999–2010 calculated using this method was $0.17\,m\,s^{-1}$. Where it is not possible to calculate a u^* threshold, a default value of $0.4\,m\,s^{-1}$ is used.

Although near-continuous meteorological data were collected, the occasional short-term gaps of < 1 h were filled by manual interpolation. Longer-term gaps in the meteorological data, caused by battery or logging failure, were filled using data from an automatic weather station at the nearby Alice Holt Research Station. Over the 12-yr period maintenance, data logging and power failure problems resulted in a mean annual loss of 18.5 % of total available flux data. Quality control, primary, secondary and LE/H despiking routines removed a further 2.6 %, whilst u^* filtering removed 17.1 %, resulting in a mean annual quality-controlled CO_2 flux data availability of 61.8 % (Table 2), and exceeding 50 % in all years.

2.5 CO_2 flux partitioning

The half-hourly quality-controlled NEE data were partitioned into gross primary productivity (GPP) and ecosystem respiration (R_{eco}) using the on-line CarboEurope gap filling tool (Reichstein et al., 2005). The dataset is split into 10-day consecutive periods, and R_{eco} is estimated using the Lloyd–Taylor regression model (Lloyd and Taylor, 1994) between nighttime CO_2 flux (global solar radiation $< 20\,W\,m^{-2}$) and air temperature. The estimated value of R_{eco} is then assigned

Table 2. Sources of annual data loss of CO_2 flux measurements for the period 1999–2010 at the Straits Inclosure, Alice Holt Forest and quality-controlled (QC) data availability (%).

Year	Power/ logging failure	QC/ despiking	u^* filtering	QC flux data
1999	13.9	2.3	17.7	66.1
2000	21.7	2.5	15.5	60.3
2001	27.0	2.5	11.0	59.5
2002	24.9	2.3	13.9	58.9
2003	18.8	3.1	23.3	54.8
2004	13.0	3.5	15.2	68.3
2005	8.2	3.9	12.7	75.2
2006	23.7	0.1	14.2	62.1
2007	19.5	2.3	19.2	59.0
2008	12.9	5.3	30.2	51.5
2009	23.9	2.3	18.5	55.3
2010	15.0	0.8	13.7	70.5
Mean	18.5	2.6	17.1	61.8

to the central time point of the averaging interval and linearly interpolated between time points. GPP is subsequently calculated as the difference between NEE and R_{eco}. By convention, NEP was defined as opposite in sign to NEE (Fig. 2).

3 Results and analysis

3.1 Climatic conditions

The average annual cycles of daily maximum air temperature (T_{max}), minimum air temperature (T_{min}) and incident solar radiation (S_g) recorded at the flux site are shown in Fig. 3a and the average daily soil moisture content and mean monthly precipitation from the nearby Alice Holt Research station in Fig. 3b. Collectively these illustrate the oceanic climate of the region, typified by mild winters, cool summers and a relatively uniform distribution of precipitation throughout the year. Using the Köppen climate classification system, the region is classified as "Cfb". The long-term (1971–2000) mean annual precipitation of 779 mm was exceeded in 8 out of the 12 yr, with the highest recorded amount falling in 2002 (1046 mm) and the lowest in 2005 (590 mm). The mean annual above-canopy solar radiation receipts were lowest in 2002 (253 W m^{-2}) and highest in 2006 (319 W m^{-2}). Long-term observations (1948–2009) from the Alice Holt weather station near the site have demonstrated a warming in mean surface air temperature (data not shown) of $\sim$0.2 °C per decade, with higher rates of warming in winter and summer than in spring and autumn. Whilst there has been no overall change in annual precipitation, there has been a slight reduction in summer and an increase in winter levels over this period.

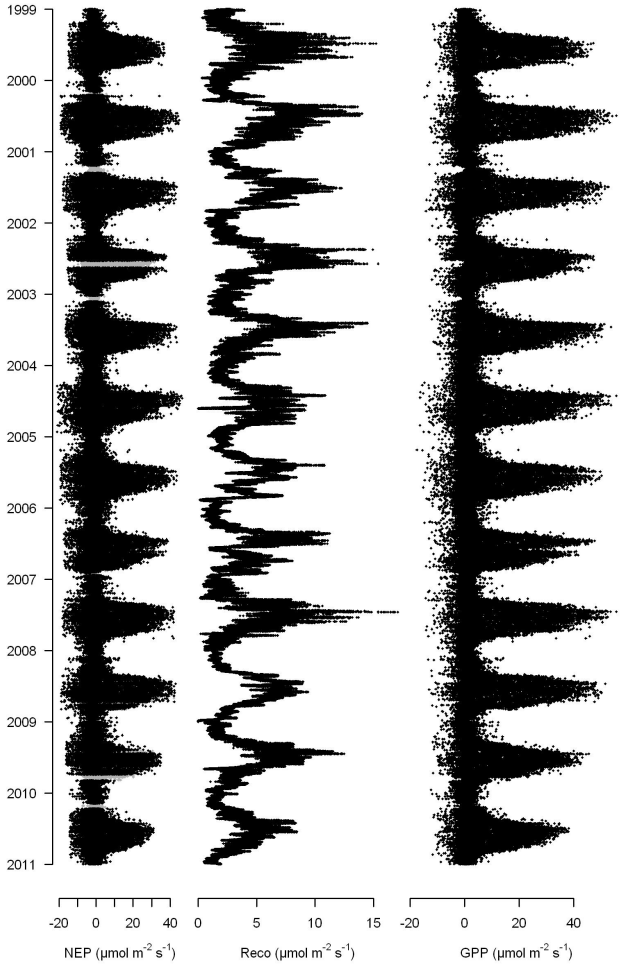

Fig. 2. Half-hourly average values of quality-controlled (black symbols) and gap-filled (gray symbols) NEP, R_{eco} and GPP for the period 1999–2010, at the oak plantation, Straits Inclosure, Alice Holt Forest.

3.2 Annual cycle of carbon fluxes

Substantial seasonal and inter-annual variations in component fluxes were measured (Fig. 2). In order to describe the mean annual carbon cycle for each of these components, data from all 12 yr were pooled (Fig. 3c). Over the winter period (December, January, February), GPP was close to zero and started to rise slowly from around day of year (DOY) 50 as a result of early bud break and leaf expansion of the shrub layer, exploiting available light. At approximately DOY 100 GPP started to rise more rapidly, coinciding with bud break and expansion of the tree canopy, peaking at around DOY 170, with a mean summer (June, July and August) value of 13.5 g C m^{-2} d^{-1}. A reduction in GPP started around DOY 200 as mean solar radiation levels declined (Fig. 3a); this reduction accelerated around the beginning of October ($\sim$ DOY 280), corresponding with the start of canopy senescence.

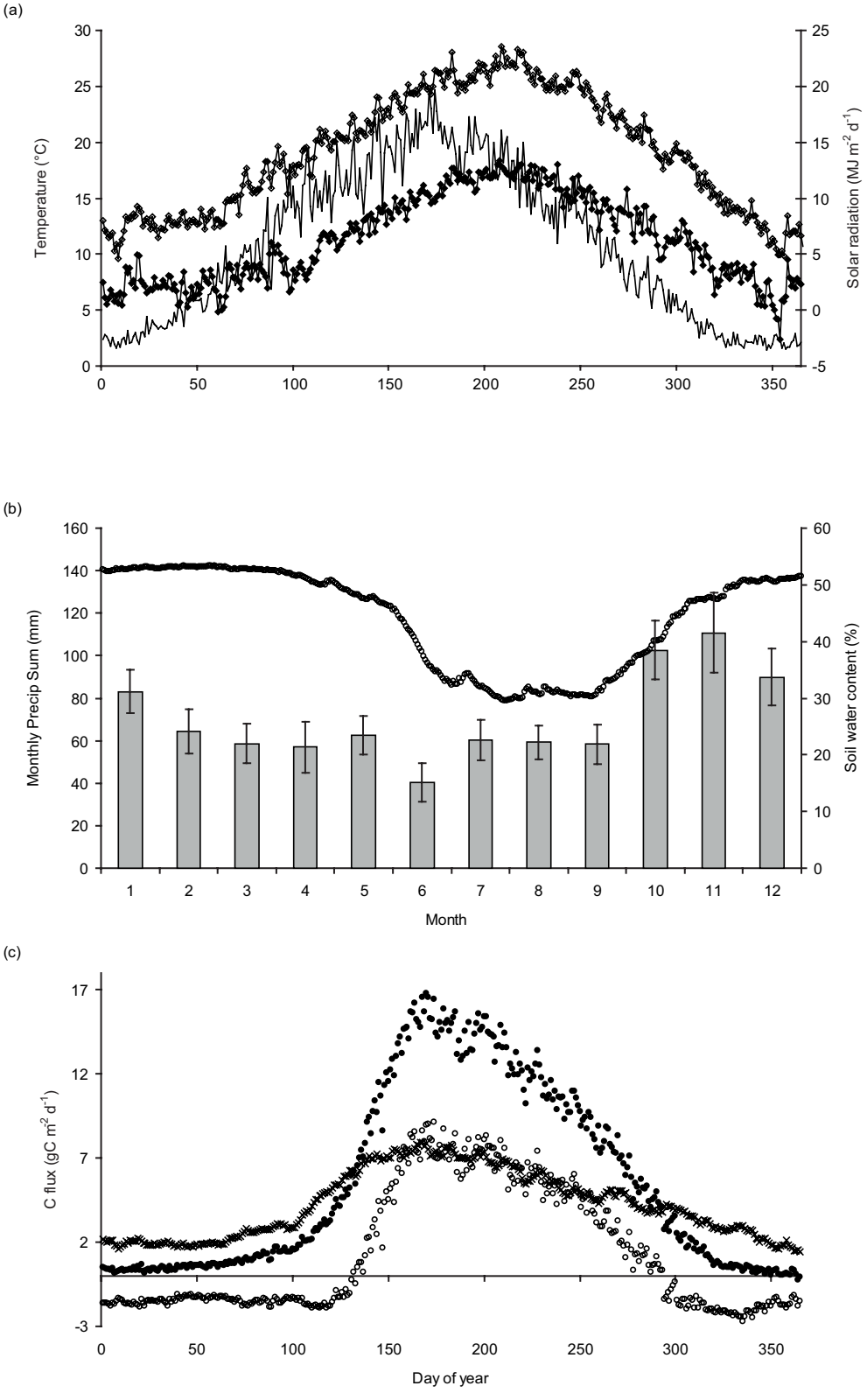

Fig. 3. Average annual cycle of key climatic variables and CO_2 flux components between 1999–2010 for the oak plantation at the Straits Inclosure, Alice Holt Forest: **(a)** T_{max} (open symbols), T_{min} (closed symbols) and incident solar radiation (solid line); **(b)** mean monthly precipitation (error bars represent ± 1 standard error, $n = 12$) and volumetric soil water content recorded under grass nearby (open symbols); and **(c)** daily GPP (solid circles), R_{eco} (crosses) and NEP (open circles).

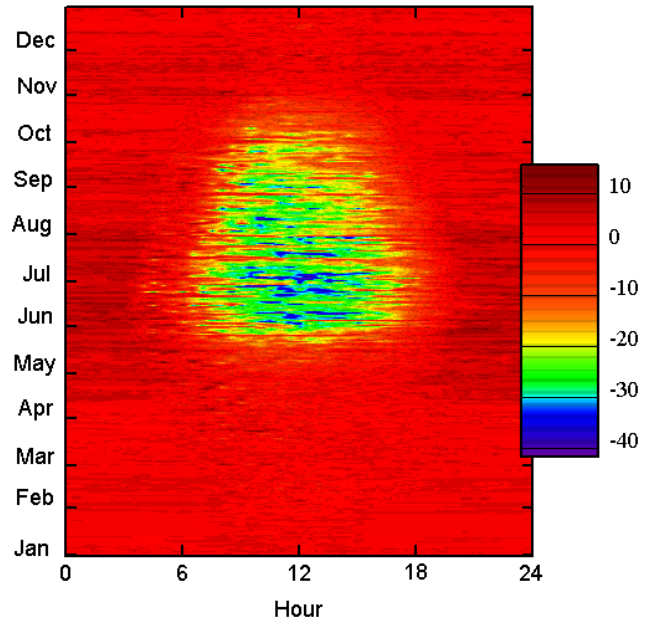

Fig. 4. A typical (2003) net ecosystem exchange (NEE) "finger-print" plot showing diurnal (x-axis) and seasonal (y-axis) CO_2 fluxes ($\mu mol\,m^{-2}\,s^{-1}$) for the oak plantation at the Straits Inclosure, Alice Holt Forest, generated by the CarboEurope on-line gap filling and partitioning tool.

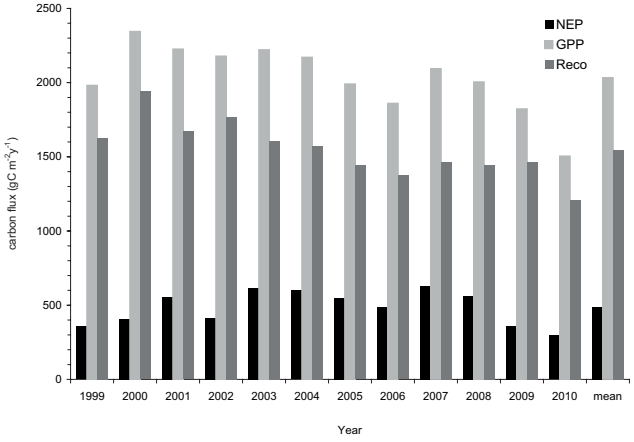

Fig. 5. Annual sum of NEP, GPP and R_{eco} for the period 1999–2010 at the oak plantation, Straits Inclosure, Alice Holt Forest

R_{eco} also demonstrated a strong seasonal cycle (Fig. 3c), with the lowest fluxes occurring over the cooler winter period at a mean rate $2.0\,g\,C\,m^{-2}\,d^{-1}$. R_{eco} stayed low until approximately DOY 70, when it began to increase slowly at first and more rapidly from DOY 100, coinciding with increases in air and soil temperature. The highest R_{eco} occurred during the warm summer months between DOY 145 and 200, with a mean summer rate of $6.7\,g\,C\,m^{-2}\,d^{-1}$. The NEP of an ecosystem is determined by the relative balance of GPP and R_{eco}. In this study daily NEP remained negative until on average DOY 132; prior to this point small increases in GPP and R_{eco} effectively cancel each other out, ensuring that NEP remains constant until approximately DOY 115. During spring (DOY 115-150) as the increase in GPP exceeded losses through R_{eco}, daily NEP rapidly turned from being negative (a CO_2 source) to positive (a CO_2 sink); over the summer, high levels of GPP relative to R_{eco} resulted in a mean NEP of $6.8\,g\,C\,m^{-2}\,d^{-1}$. On a daily timescale the forest continued to act as a net CO_2 sink until on average DOY 297, after which it reverted to being a source. Over the 12-yr measurement period, mean daily winter (December–February) NEP was $-1.6\,g\,C\,m^{-2}\,d^{-1}$.

The diurnal and seasonal changes of NEE for a typical year (2003) are shown in the "finger print" plot (Fig. 4). Maximum CO_2 sequestration occurred during spring and summer daylight hours (green through to dark blue). The asymmetrical shape of the NEE "pulse" within the year was caused by the rapid increase in net CO_2 uptake in the spring followed by a more gradual decline at the end of the growing season. In addition, higher CO_2 uptake fluxes are evident during the morning than in the afternoon during September, indicating the possibility of moisture stress.

3.3 Inter-annual variation in NEP, GPP and R_{eco}

The carbon budget and partitioned fluxes were calculated for each year of the study period (Fig. 5 and Table 3). Annual NEP varied from $296\,g\,C\,m^{-2}\,yr^{-1}$ (2010) to a maximum of $629\,g\,C\,m^{-2}\,yr^{-1}$ (2007), with a 12-yr average of $486 \pm 73\,g\,C\,m^{-2}\,yr^{-1}$ (95 % CI). The maximum year-to-year variation in NEP was therefore $333\,g\,C\,m^{-2}\,yr^{-1}$. The growing season length (GSL), here defined as the number of days between the first and last day where the integrated 3-day NEP was positive (a net sink of carbon), also varied considerably from year to year (Table 4). The average GSL was 165 days, (±6 days, 95 % CI); the longest GSL occurred in 2007 (186 days) and the shortest in 2005 (153 days).

The inter-annual variation in the calculated R_{eco} was large (from a minimum of 1210 to a maximum of $1940\,g\,C\,m^{-2}\,yr^{-1}$, Table 3), and the standard deviation (SD) was larger than that for NEP (192 and $115\,g\,C\,m^{-2}\,yr^{-1}$, respectively, Table 3). Annual GPP ranged from $1506\,g\,C\,m^{-2}\,yr^{-1}$ (2010) to $2346\,g\,C\,m^{-2}\,yr^{-1}$ (2000), with $SD = 223\,g\,C\,m^{-2}\,yr^{-1}$. As R_{eco} is driven in part by preceding GPP, it could be argued that the NEP budget for any given year should be calculated over the growing season year (i.e. 1 April through to 31 March in the following year). However, our results show that this approach had very little effect on the annual sums in most years, and only in 2005 was there a noticeable difference (Table 3).

Anomalies from the long-term monthly means in GPP, R_{eco} and associated environmental variables were calculated (Fig. 6). GPP was high during the spring and summer of 2000 probably because of the combined effect of high peak LAI ($7.7\,m^2\,m^{-2}$) and average solar radiation receipts. GPP was

Table 3. Annual values 1999–2010 of carbon flux components for the oak plantation at the Straits Inclosure in Alice Holt Forest. Radiation-use efficiency (RUE) is calculated as GPP/incident solar radiation. NEP_{gsy} is the sum of NEP in the growing season year, i.e. 1 April through to 31 March in the following year. Peak LAI was back calculated from cumulative LAI measured using litterfall traps sampled bi-weekly.

Year	NEP $g\,C\,m^{-2}$	R_{eco} $g\,C\,m^{-2}$	GPP $g\,C\,m^{-2}$	R_{eco}/GPP	NEP/GPP	RUE $g\,C\,MJ^{-1}$	NEP_{gsy} $g\,C\,m^{-2}$	Peak LAI $m^2\,m^{-2}$
1999	357	1625	1983	0.820	0.180	0.486	345	6.49
2000	406	1940	2346	0.827	0.173	0.616	405	7.72
2001	557	1670	2227	0.750	0.250	0.575	538	6.94
2002	412	1767	2180	0.811	0.189	0.554	426	5.52
2003	617	1606	2223	0.722	0.278	0.542	613	6.17
2004	600	1573	2172	0.724	0.276	0.563	585	6.55
2005	551	1441	1992	0.723	0.277	0.510	630	4.97
2006	488	1374	1862	0.738	0.262	0.464	466	5.42
2007	629	1466	2094	0.700	0.300	0.529	664	6.47
2008	563	1442	2006	0.719	0.281	0.520	518	6.21
2009	359	1465	1824	0.803	0.197	0.458	367	4.4
2010	296	1210	1506	0.804	0.196	0.414	321	4.18
Mean	486	1548	2034	0.762	0.239	0.520	490	5.92
SEM*	33.3	55.6	65.8	0.01	0.01	0.02	34.0	0.32
SD	115	192	223	0.01	0.05	0.04	117.67	1.05

* SEM = standard error of the mean

Table 4. Onset of growing season (OGS), end of growing season (EGS) and growing season length (GSL) defined by the start and end of net CO_2 uptake, at the Straits Inclosure, Alice Holt Forest.

Year	OGS (DOY)	EGS (DOY)	GSL (days)
1999	132	297	165
2000	135	291	156
2001	132	303	171
2002	135	291	156
2003	126	300	174
2004	132	291	159
2005	141	294	153
2006	138	312	174
2007	117	303	186
2008	129	297	168
2009	129	285	156
2010	132	297	165
Mean	132	297	165
SEM	1.8	2.1	2.8
SD	6.1	7.2	9.9

not adversely affected by the major Europe-wide drought year in 2003, and the year had the second highest GPP sum over the entire 12-yr period probably because of the above-average solar radiation levels. Although 2003 had the lowest precipitation total, this followed a wet end to 2002 (Fig. 6a) and soil moisture (Fig. 6c) did not start to decline below the long-term monthly mean until July. Precipitation was also lower than average for most of 2005; although summer soil moisture levels did not fall as low as in 2003, the decline started a month earlier in the year, which combined with the lower levels of solar radiation caused a reduction in summer GPP in 2005. It is likely that low R_{eco} values in late summer/early autumn, as occurred in 2003, 2005 and 2006, can be attributed to low soil moisture levels (Fig. 6c).

GPP was low in 2009 and 2010 because of considerable damage to the forest canopy following a major outbreak of defoliating moth caterpillars, mostly *Tortrix viridana* L., but also *Operophtera brumata* L., early in the year (Pitman et al., 2010). This was despite an increase in incident solar radiation of 4 % in 2009 and 7 % in 2010 received during the May to July period of each year. The infestation caused a reduction in peak LAI values (Table 3) from the long-term mean of 26 % in 2009 ($4.40\,m^2\,m^{-2}$) and 30 % in 2010 ($4.18\,m^2\,m^{-2}$), which resulted in a reduction of GPP by 5 % in 2009 and 33 % in 2010.

The overall time trends in annual GPP, R_{eco} and NEP were tested by linear regression against year. Although there was no apparent long-term trend in the annual NEP ($p = 0.89$), this resulted from similar significant decreases in both GPP ($-46.1\,g\,C\,m^{-2}\,yr^{-1}$, standard error (s.e.) 13.7, $p < 0.01$) and R_{eco} ($-44.7\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 9.2, $p < 0.001$) over time. If the last two annual values from the insect-affected years of 2009 and 2010 were omitted, there was a significant positive trend in NEP ($+21.0\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 8.5, $p < 0.05$), because the declining trend in GPP was reduced to $-24.2\,g\,C\,m^{-2}\,yr^{-1}$, although the declining trend in R_{eco} was not affected ($-45.2\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 12.2, $p < 0.01$). However, none of these changes in slope when 2009 and 2010 values were omitted were significant because of their large standard errors.

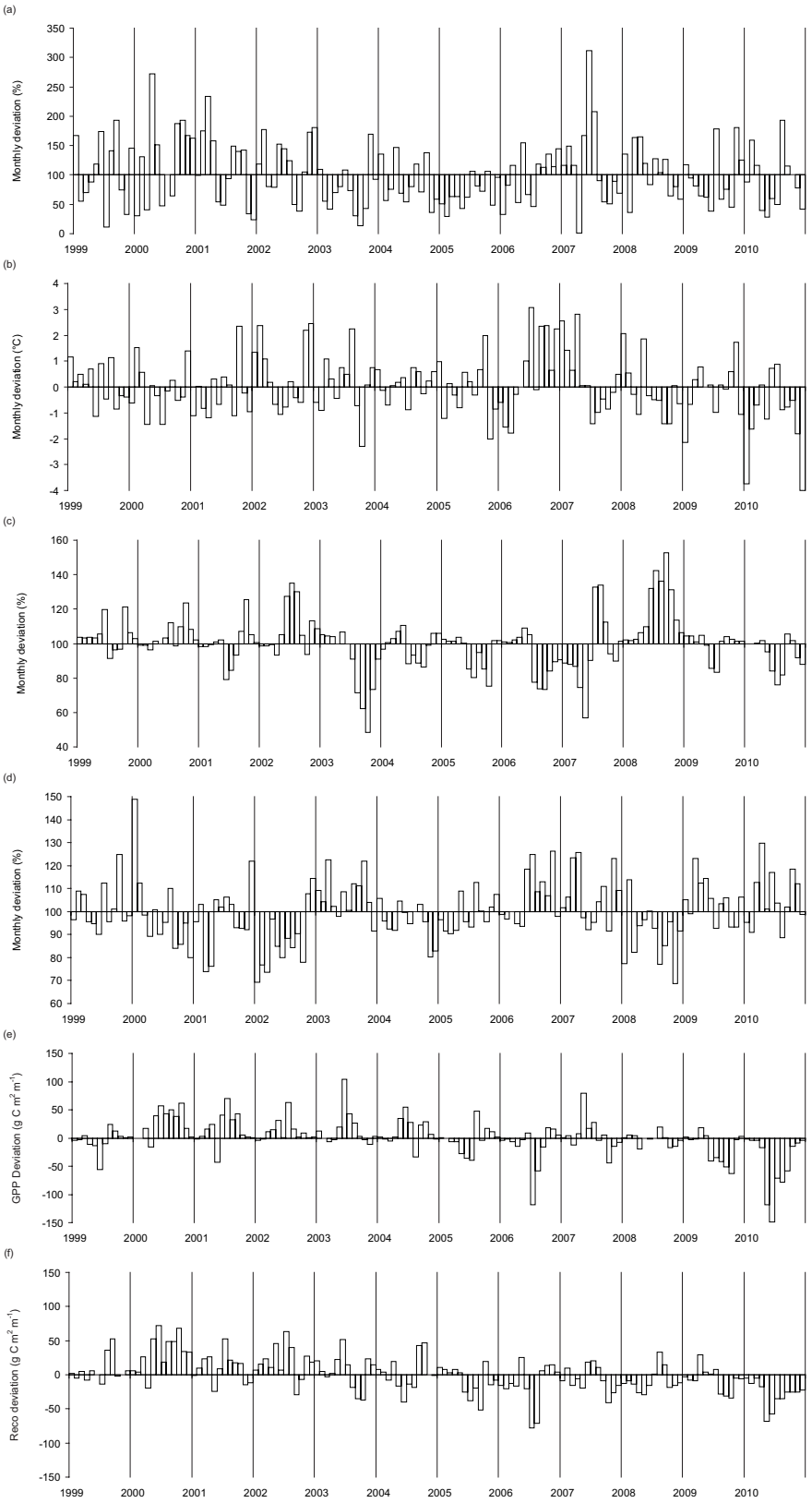

Fig. 6. Deviation from the 12-yr monthly average (1999–2010) for key climatic variables and partitioned CO_2 flux components at the oak plantation woodland, Straits Inclosure, Alice Holt Forest: **(a)** precipitation, **(b)** air temperature, **(c)** soil moisture, **(d)** solar radiation, **(e)** GPP and **(f)** R_{eco}.

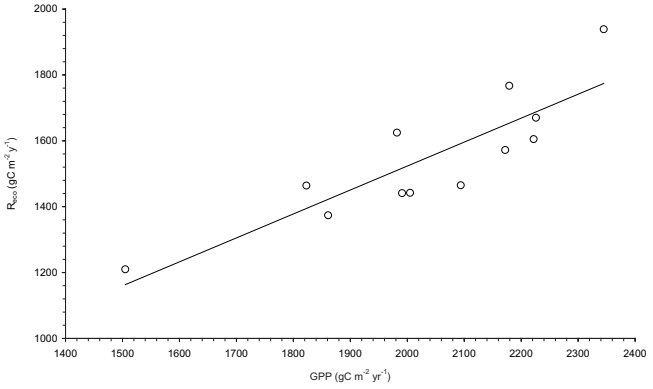

Fig. 7. Relationship between annual R_{eco} and annual GPP ($r^2 = 0.74$, $p < 0.001$).

3.4 Environmental controls of GPP, R_{eco} and NEP

NEP is the relatively small difference between the two much larger fluxes of GPP and R_{eco} (Baldocchi, 2008), which were shown to be tightly correlated (Fig. 7 and Table 3), with a mean R_{eco}/GPP ratio of 0.76 ($\pm$ 0.03 CI). Therefore, in order to understand the possible causes of inter-annual variation in NEP, it is necessary to explore the causes of variation in GPP and R_{eco}.

On an annual time scale, GPP was weakly correlated with mean annual air temperature ($r^2 = 0.27$, $p < 0.1$) but not with growing season incident solar radiation ($r^2 = 0.13$, $p > 0.1$) or GSL ($r^2 < 0.1$, $p > 0.1$) (data not shown). Therefore radiation use efficiency (RUE = GPP/incident solar radiation) varied between years (mean = 0.52 g C MJ^{-1}, 12 % CV, Table 3). There was a stronger correlation between GPP and intercepted solar radiation ($S_g{}^i$, $r^2 = 0.46$, $p < 0.05$, Fig. 8a) resulting in less interannual variation in radiation use efficiency calculated on an intercepted basis (mean = 0.88 g C MJ^{-1}, 8.5 % CV). The strongest correlation was between annual GPP and peak LAI ($r^2 = 0.70$, $p < 0.001$, Fig. 8b). Peak LAI showed a significant linear decline over time (-0.208 LAI yr^{-1}, $r^2 = 0.51$, $p < 0.01$), and this resulted in reduced fractional radiation interception and reduced annual GPP and R_{eco} over time. Resulting seasonal differences in RUE for years of contrasting LAI are illustrated in Fig. 9 . The year with highest observed LAI, 2000, had a higher than average RUE during the June–October period; conversely, 2009 with low LAI showed a below average RUE.

Coefficients of an exponential function were derived by fitting monthly R_{eco} and mean monthly air temperature (Table 5). The high overall degree of correlation (mean $r^2 = 0.82$) within each year is not surprising given the method by which R_{eco} was estimated (see Sect. 2.5). However, this approach is useful in highlighting the variation in response between years. Figure 10 shows the relationship for years of contrasting R_{eco}, i.e. high (2000 and 2002) and

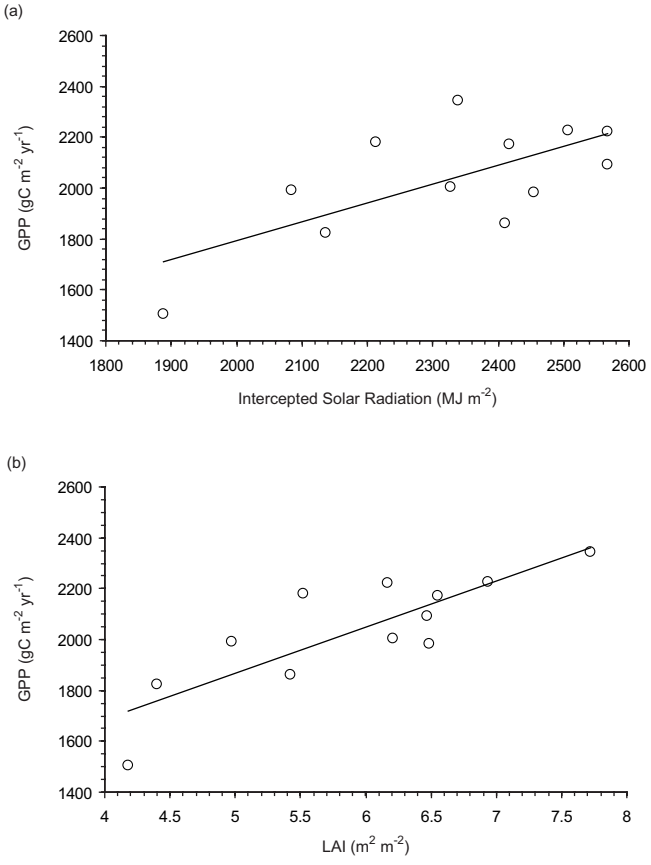

Fig. 8. Relationship between **(a)** annual GPP and intercepted solar radiation ($r^2 = 0.46$, $p < 0.05$) and **(b)** annual GPP and peak LAI ($r^2 = 0.7$, $p < 0.001$).

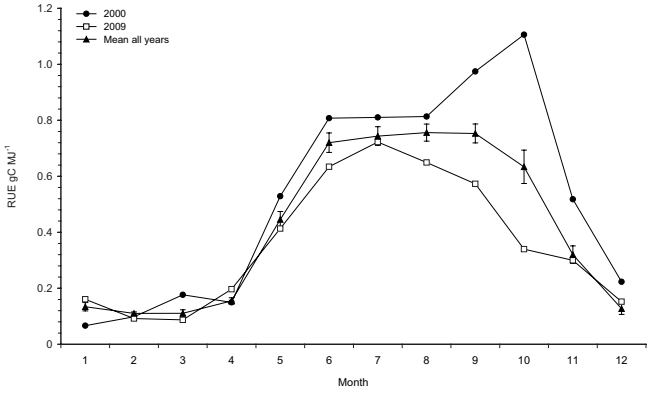

Fig. 9. Monthly RUE for contrasting years of high GPP (2000) and low GPP (2009).

low (2006 and 2010). It is evident that the years of high annual R_{eco} showed an enhanced sensitivity of monthly R_{eco} to temperature and, conversely, a lower sensitivity during the years of low annual R_{eco}. When the monthly R_{eco} values are separated between growing season (May–October, inclusive) and non-growing season months, it becomes clear

Table 5. Coefficients of an exponential model-fitted monthly R_{eco} to mean monthly air temperature, calculated mean Q10 values and r^2 values for the Straits Inclosure, Alice Holt Forest. r^2 values are also shown for exponential regressions for the non-growing (November–March) and growing (April–October) season months, separately.

Year	Intercept	e	r^2	Q10	Non-growing season r^2	Growing season r^2
1999	36.12	0.114	0.895	3.13	0.973	0.537
2000	41.89	0.119	0.815	3.30	0.469	0.110
2001	40.80	0.108	0.881	2.95	0.936	0.571
2002	35.04	0.122	0.740	3.38	0.878	0.242
2003	49.51	0.084	0.688	2.32	0.692	0.319
2004	41.25	0.100	0.836	2.73	0.925	0.001
2005	47.66	0.081	0.719	2.26	0.864	0.009
2006	38.69	0.086	0.655	2.37	0.751	0.200
2007	19.79	0.155	0.924	4.72	0.525	0.739
2008	24.77	0.139	0.948	4.01	0.676	0.969
2009	36.88	0.103	0.777	2.81	0.801	0.207
2010	39.90	0.088	0.934	2.41	0.765	0.768
Mean	38.22	0.107	0.818	3.00	0.771	0.389
SEM	2.53	0.01	–	0.22	–	–
SD	8.77	0.62	–	0.78	–	–

that the relationship with temperature is much more consistent in the non-growing season (Table 5). In several years there is no evident relationship between growing season R_{eco} and temperature, suggesting that other factors are more influential, accounting for the reduction in sensitivity to temperature shown in Fig. 10. This sensitivity when quantified as the apparent Q10 value was found to be strongly related to the mean summer (July–September) soil moisture content (Fig. 11, $y = 0.099x - 0.06$; $r^2 = 0.78$). This analysis indicates that high rates of R_{eco} occur at this site under the combined conditions of high air and soil temperature and higher than average summer soil moisture.

As noted above, annual NEP did not show any clear trends over time. While annual NEP sums were related to neither the single variables of annual incident radiation (S_g), precipitation (P), average air temperature, mean summer soil moisture content (SM) nor peak leaf area index, NEP was weakly related to intercepted radiation, ${S_g}^i$ ($r^2 = 0.421$, $p < 0.05$). When possible drivers were analysed with multiple regression, the best linear model derived was NEP $\propto {S_g}^i + P +$ SM ($r^2 = 0.715$, $p = 0.014$), accounting for more than 70 % of the variation in NEP.

3.5 NEP comparison with biometric-based estimates

Regular tree mensuration assessments have been carried out as part of the ECN vegetation monitoring protocol (Sykes and Lane, 1996) in plots within the potential EC (eddy covariance) footprint (Table 1), therefore enabling a comparison with the EC-based estimates of NEP. The mensuration data were used to estimate stem volumes and above-ground biomass, using empirical biometric relationships derived from sets of 10 oak trees harvested and weighed in the inclosure in both 2005 and in 2009. Assuming a C content of dry weight of 50 % (Broadmeadow and Matthews, 2003) gives a mean annual estimated increase between 1997 and 2011 in above-ground biomass of 260 g C m^{-2} yr^{-1} (canopy trees only). Using relationships found by McKay et al. (2003) specifically for oak trees, the below-ground biomass increment was estimated as 87 g C m^{-2} yr^{-1}. Thus the mean annual (biometric) estimated C uptake was 347 g C m^{-2} yr^{-1}, 71 % of the mean NEP estimated from EC fluxes (486 g C m^{-2} yr^{-1}).

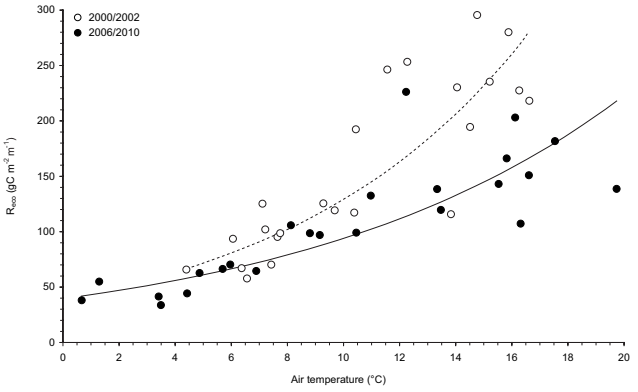

Fig. 10. Relationship between the monthly sum of R_{eco} and mean monthly air temperature for years of high (2000 and 2002; $r^2 = 0.75$) and low (2006 and 2010; $r^2 = 0.78$) annual R_{eco}.

4 Discussion

4.1 Annual C budget of woodlands in Britain and Ireland

Using eddy covariance (EC) measurements we have provided a 12-yr time series of partitioned forest CO_2 fluxes and quantified the inter-annual variation of these partitioned fluxes (Fig. 5) for a managed oak woodland in south-eastern England, revealing important differences in their seasonal phase and amplitude (Fig. 3c). Although the accuracy of eddy covariance measurements in establishing C balances has been questioned because of the problems of filling inevitable data gaps, the various methodological corrections required, difficulties in measuring nighttime fluxes, and advection problems, some comparisons have shown good agreement with direct measurements of changes in C stocks (Gough et al., 2008; Thomas et al., 2011). Whilst we do not have the detailed representative component stock change estimates, as in the exemplary work by Butt et al. (2009) or Gough et al. (2008), the available mensuration data suggest NEP values that are similar, but 29 % lower than those estimated by eddy covariance (EC). However, this biometric estimate includes neither the substantial C uptake by the woody understorey, which might be ∼ 10 % (Moore et al., 2007), nor any

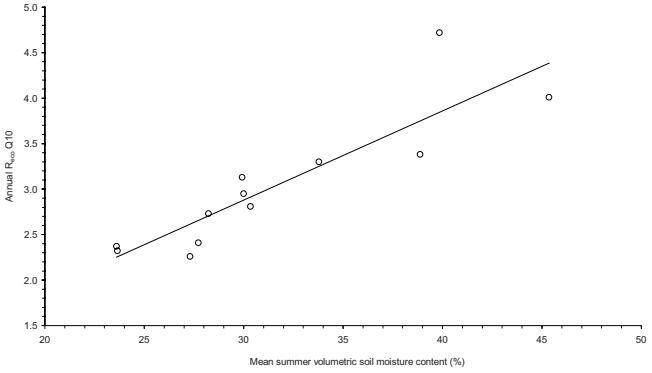

Fig. 11. Relationship between annual R_{eco} Q10 and summer volumetric soil moisture content measured at a depth of 10 cm at the Alice Holt Research Station ($r^2 = 0.78$, $p < 0.001$). Annual Q10 values were calculated from the coefficients of an exponential function fitted to monthly R_{eco} and mean monthly air temperature.

increase in soil organic C content, estimated in this woodland to be 34 g C m^{-2} yr^{-1} (Benham et al., 2012), about 7 % of EC NEP. If these components are included, agreement to within 10–15 % gives some confidence in the NEP values derived from EC data, given the low precision of the biometric approach.

Between 1999 and 2010, the forest acted as a substantial net C sink with a mean NEP of 486 g C m^{-2} yr^{-1}, further evidence that temperate deciduous woodlands actively contribute to the global terrestrial C sink (Luyssaert et al., 2007). Furthermore, the results from this study provide a good basis for understanding the processes of CO_2 exchange within deciduous woodlands under British conditions, which to date have been poorly characterised. Despite the fact that there are more than 30 forest EC flux sites (Clement et al., 2012) currently active across Europe, Britain has only a few, of which only two can be considered long-term studies, (i.e. > 5 yr): this Alice Holt site, and the Griffin Forest site in central Scotland, located in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation, established in 1997 (Clement et al., 2012). Between 1997 and 2001, average NEP of that young coniferous forest was 721 g C m^{-2} yr^{-1}, which is substantially larger (+48 %) than the NEP observed in the current study. Whilst partitioned flux estimates from Griffin Forest indicate very similar levels of R_{eco} (1533 g C m^{-2} yr^{-1}) to the current study (1548 g C m^{-2} yr^{-1}), despite differing soil types, the longer growing season and higher carbon use efficiency of coniferous forests meant that GPP at Griffin was substantially higher (+11 %). Under milder conditions than those experienced at the Griffin Forest site, the NEP of Sitka spruce in Dooary, central Ireland, has been shown to be even higher (830–890 g C m^{-2} yr^{-1}; Black et al., 2007).

Although the mean NEP reported here is at the high end of the range reported from other comparable temperate deciduous or semi-deciduous woodlands (Table 6), it is not the highest and has been exceeded at other European deciduous sites. NEP of 660 g C m^{-2} yr^{-1} was reported at the Collelongo Forest site in Italy (Valentini et al., 2000) and NEP of 550 g C m^{-2} yr^{-1} from an oak sub plot at the Kannenbruch Forest in Germany (Kutsch et al., 2005). However, it should be noted that both of these values were derived from much shorter time series than this study, and in half the 12 yr at Alice Holt the NEP was between 550 and 650 g C m^{-2} yr^{-1} (Table 3).

A site where comparable EC flux measurements have been made in deciduous woodland is that at Wytham Woods in Oxfordshire (Thomas et al., 2011), where a relatively short-term study showed very similar rates of GPP to this study (2110 g C m^{-2} yr^{-1}). It is noteworthy that the Straits site shows one of the larger mean annual GPP values in any of the long-term temperate or boreal forests so far reported (see Table 6). Only the two evergreen conifer plantations at Griffin and Dooary have higher GPP values. However, substantially higher R_{eco} rates at Wytham Woods (1980 g C m^{-2} yr^{-1}) resulted in a much lower mean annual NEP (130 g C m^{-2} yr^{-1}). The Straits Inclosure and Wytham Woods have had contrasting histories; whereas our study site has been managed as commercial forest, with regular interventions, it is likely that the higher levels of R_{eco} observed at Wytham Woods are a result of less intensive management over the last few decades (Kirby, 2010), resulting in greater levels of decomposing deadwood and possibly higher level of heterotrophic respiration due to enhanced soil activity and C levels.

No trend in NEP was observed at our site over the 12 yr, although there were declining trends in both GPP and R_{eco}. Recent data for 2011 are consistent with these trends. This contrasts with the observed increasing NEP trend of 23 g C m^{-2} yr^{-1} observed over 14 yr in a similarly aged beech stand in Denmark, attributed to increasing GPP (Pilegaard et al., 2011).

4.2 Inter-annual variation in NEP, GPP and R_{eco}

Understanding of the sources of inter-annual variation in NEP, GPP and R_{eco} within forest ecosystems is improving as the number of EC forest sites where multi-year records are available increases. In this study, the 12-yr measurement period showed quite high inter-annual variations in NEP, GPP and R_{eco} (SD of 115, 223 and 192 g C m^{-2} yr^{-1} respectively). This may be because of the influence of the variable temperate oceanic climate, but it may also be because the length of record means that there is an increased likelihood of including anomalous or extreme climate years and episodes of biotic stresses such as pests and diseases. Although the variation in GPP and R_{eco} is large compared to similar sites across a range of forest types (Table 6), the close linkage between R_{eco} and GPP resulted in smaller variation in NEP, similar to that found at other sites (Table 6).

Within temperate forests a number of biotic and abiotic factors have been shown to have a controlling effect on GPP,

Table 6. Published multi-annual values of NEP, GPP and R_{eco} for a range of temperate and boreal forest ecosystems

Site	Country	No of years	Measurement period	NEP $g C m^{-2} yr^{-1}$	GPP $g C m^{-2} yr^{-1}$	R_{eco} $g C m^{-2} yr^{-1}$	Forest Type	Authors
Alice Holt	UK	12	1999–2010	486 (115)	2034 (228)	1548 (192)	Temperate deciduous oak plantation	Present study
Griffin	UK	5	1997–2001	721 (60)	2253 (83)	1533 (37)	Temperate conifer plantation	Clement et al. (2012)
De Inslag	Belgium	6	1997–2002	−91 (na)	1234 (na)	1326 (na)	Mixed temperate	Carrara et al. (2003)
Lille Bøgeshov	Denmark	14	1996–2009	156 (103)	1727 (136)	1570 (97)	Temperate beech	Pilegaard et al. (2011)
SMEAR II	Finland	10	1999–2007	206 (38)	1031 (54)	825 (39)	Boreal Scots pine	Ilvesniemi et al. (2009)
Hesse	France	10	1995–2005	386 (171)	1397 (192)	1011 (138)	Temperate beech	Granier et al. (2008)
Puéchabon	France	6[b]	2001–2006	278 (117)	1317 (151)	1018 (68)	Evergreen Mediterranean forest	Allard et al. (2008)
Dooary	Ireland	8	2000–2006[c]	886 (20)	2311 (145)	1445 (133)	Temperate conifer plantation	Saunders et al. (2012)
Borden Forest	Canada	8	1996–2003	141 (112)	1118 (92)	976 (67)	Mixed hardwood and conifer	Teklemariam et al. (2009)
Northern Old Black Spruce	Canada	10	1994–2004	1.8 (41)	706 (57)	713 (79)	Black spruce/veneer bog	Dunn et al. (2007)
Harvard Forest	USA	9	1993–2000	201 (36)	1297 (99)	1099 (91)	Mixed deciduous	Barford et al. (2001)
Harvard Forest[a]	USA	13	1992–2004	245 (100)	1400 (164)	1153 (105)	Mixed deciduous	Urbanski et al. (2007)
Akou	Japan	3	2001–2003	615 (189)	1759 (220)	1144 (135)	Warm temperate evergreen broad-leaved	Kosugi et al. (2005)
Takayama	Japan	9	1994–2002	237 (92)	978 (120)	742 (36)	Cool temperate deciduous forest	Saigusa et al. (2005)
Tomakomai National Forest	Japan	3	2001–2003	212 (44)	1673 (60)	1461 (43)	Larch plantation	Hirata et al. (2007)

Where NEP data were not available, NEE has been used; figures in brackets are standard deviation;
[a] based on ecological year;
[b] of this 9-yr study, only 6 full years of data were available;
[c] based on the pre-thinning period.

including light interception, seasonal phenological development, temperature and moisture availability (Reichstein et al., 2007). The ratio of CO_2 uptake to available light is a key variable, and has been shown to be influenced by a variety of environmental conditions and stresses including stand age, species composition, soil fertility, nutrient status (Gower et al., 1999) and the ratio of diffuse to total incident radiation (Jenkins et al., 2007; Alton, 2008). Here, the annual mean RUE varied between 0.62 and 0.41 $g C MJ^{-1}$ incident radiation (2000 and 2010 respectively; Table 3), averaging 0.52 $g C MJ^{-1}$. A comparison with other sites is made difficult as there is no common definition of RUE. Some studies have used net primary productivity as the numerator; others have used GPP (Schwalm et al., 2006). In years with low peak LAI, monthly RUE values were low (Fig. 9), particularly later in the year. It is unlikely that, over such monthly periods, variation in the ratio of diffuse to total incident radiation was a major contributor to this effect. Peak LAI explained a large proportion of the inter-annual variation in annual GPP ($r^2 = 0.7$; Fig. 8) because of its direct relationship with light interception and canopy photosynthesis; a similar response to that shown by Longdoz et al. (2010) across a range of forest sites in France. Furthermore, the trend of declining peak LAI over time at this site led to parallel declines in GPP and R_{eco}. We can offer no explanation for this long-term decline in peak LAI. Interestingly, when annual R_{eco} totals are separated into growing season and non-growing season periods, the declining trend is only found in the growing season R_{eco}, which comprises 71 % (±3 % CI) of the annual total. This emphasises the strong linkage between R_{eco} and GPP within a growing season.

Growing season length has also been shown to be an important control factor in ecosystem C balance both at the individual site level (e.g. Carrara et al., 2003; Granier et al., 2008) and across a range of forest types (Baldocchi and Xu, 2005). However, at this site neither NEP nor GPP was correlated with onset of growing season or length of growing season. This is similar to the findings of Dunn et al. (2007) who found no correlation between longer growing seasons and net C uptake (at a boreal black spruce forest), which they suggested was due to corresponding increases in ecosystem respiration offsetting increased GPP during longer growing seasons.

The importance of indirect climatic events such as insect-induced canopy defoliation is becoming evident from the growing network of long-term forest EC studies (Allard et al., 2008; Pilegaard et al., 2011). In this study the observed reduction in NEP that occurred in 2009 and 2010 could in part be attributed to the major outbreak of defoliating moth caterpillars, which caused a significant reduction in peak LAI. In addition, there are likely to have been some effects of the oak powdery mildew (*Erysiphe alphitoides*) infection of leaf regrowth on a number of oak trees within the study

area in 2009 and 2010 (Heinemeyer at al., 2012) and the occurrence of a late and damaging air frost on day 127 in 2010.

Understanding the determinants of R_{eco} is complicated because it is governed by several different above- and belowground processes, each responding to a set of environmental variables. The ratio of R_{eco}/GPP was relatively constant (0.76 ± 0.02 CI) and was similar to the average value of 0.80 reported by Law et al. (2002) for a range of forest types. In the absence of auxiliary measurements, it is impossible to separate total R_{eco} into its different components. However in a parallel study at the same site, between 2007 and 2010, soil CO_2 efflux was estimated to be $740 \pm 43\,g\,C\,m^{-2}\,yr^{-1}$ (Heinemeyer at al., 2012), accounting for $\sim 53\,\%$ of total R_{eco} over the same period. Other studies have estimated a larger contribution by soil autotrophs and heterotrophs to total R_{eco}. For example, Knohl et al. (2008) reported a range of 79–88 % for another temperate deciduous forest. At the annual scale, mean monthly air temperature explained most of the annual variability in R_{eco} ($r^2 = 0.81$, Table 5). Non-growing season (winter) R_{eco} was tightly correlated with air temperature (mean $r^2 = 0.77$), which we attribute to the dominance of heterotrophic respiration during this period. During the growing season the relationship was weaker and varied substantially between years because of the influence of soil moisture. There was more interannual variation in this relationship during the growing season ($r^2 = 0.39$). This type of response has been demonstrated across a range of other forest sites (Law et al., 2002) and is probably because, under conditions of moderate reduced water content, microbial respiration is limited by the diffusion of soluble organic substrates (Epron et al., 1999), particularly in the near-surface layers. The autotrophic respiration component is less likely to be affected by moderate reductions in water content because of the deeper rooting depth (Borken et al., 2006).

The 12-yr continuous dataset presented here for the first time shows that this deciduous forest ecosystem located in southeast Britain acted as a substantial sink for carbon, with a mean up take of $486\,g\,C\,m^{-2}\,yr^{-1}$ (95 % CI of $\pm 73\,g\,C\,m^{-2}\,yr^{-1}$). Our EC-based estimates of NEP are relatively closely matched by mensuration-based estimates, providing confidence in our measurements. Year-to-year variation in NEP was largely explained by changes in the contributory, yet opposing, partitioned fluxes of GPP and R_{eco}, and the main biological and environmental drivers of these have been discussed. The study has also identified the important effect that biotic damage such as insect defoliation can have on the carbon flux dynamics of forests.

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Effects of management thinning on CO_2 exchange by a plantation oak woodland in south-eastern England

Matthew Wilkinson[1], **Peter Crow**[2], **Edward L. Eaton**[1], **and James I. L. Morison**[1]

[1]Forest Research, Centre for Sustainable Forestry and Climate Change, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK
[2]Forest Research, Centre for Ecosystems, Society and Biosecurity, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

Correspondence to: Matthew Wilkinson (matthew.wilkinson@forestry.gsi.gov.uk)

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Abstract. Forest thinning, which removes some individual trees from a forest stand at intermediate stages of the rotation, is commonly used as a silvicultural technique and is a management practice that can substantially alter both forest canopy structure and carbon storage. Whilst a proportion of the standing biomass is removed through harvested timber, thinning also removes some of the photosynthetic leaf area and introduces a large pulse of woody residue (brash) to the soil surface, which potentially can alter the balance of autotrophic and heterotrophic respiration. Using a combination of eddy covariance (EC) and aerial light detection and ranging (lidar) data, this study investigated the effects of management thinning on the carbon balance and canopy structure in a commercially managed oak plantation in the south-east of England. Whilst thinning had a large effect on the canopy structure, increasing canopy complexity and gap fraction, the effects of thinning on the carbon balance were not as evident. In the first year post thinning, the peak summer photosynthetic rate was unaffected by the thinning, suggesting that the better illuminated ground vegetation and shrub layer compensated for the removed trees. Peak summer photosynthetic rate was reduced in the thinned area between 2009 and 2011, but there was no significant difference between sectors. Ecosystem respiration fluxes increased in the thinned relative to the unthinned area in the post-thinning phase.

1 Introduction

In England, woodlands cover 10.0 % of the land surface area, with the majority (0.78 Mha) comprising broadleaved woodland (Forestry Commission, 2013). The total carbon stock in the forest biomass was estimated to be 105.4 Mt C in 2011 (Forestry Commission, 2014), with 27.7 and 77.7 Mt C in conifer and broadleaved woodlands respectively. Much of this broadleaved woodland is in small areas, with 51 % in woodlands < 20 ha (Forestry Commission, 2013) and a little more than half (57 %) of these deemed to be under active management (Forestry Commission England, 2014). As forests are such large stores of carbon, the effects of disturbance (such as harvesting) are of considerable interest (see, e.g., Amiro et al., 2010). If more woodlands are brought back into management and thinning or felling is carried out, then the carbon balance may be affected.

Thinning is a forestry practice that aims to manage competition between trees in order to improve the quality, productivity, yield and form of the final tree crop and to provide an economic return before final felling. In Britain, two main types of thinning are practised: low thinning and crown thinning, with intermediate thinning a combination of these. In low thinning, suppressed and subdominant trees are removed, along with those from the smaller diameter classes, thereby reducing the competition experienced by the larger, more valuable trees. Crown thinning aims to reduce the competition from other larger trees (dominant and co-dominant). When trees of poorer growth are removed along with some dominant individuals to open the canopy, it can be classed as intermediate thinning (Kerr and Haufe, 2011).

A few studies have considered the impacts of thinning and other aspects of the forest management cycle on forest carbon balances using the eddy covariance technique (EC) (e.g. Vesala et al., 2005; Payeur-Poirier et al., 2012; Saunders et al., 2012). However, it is logistically challenging to manipulate forest stands on the scale required to facilitate EC stud-

ies. One approach is to thin the entire forest stand and analyse the pre- and post-thinning phases separately (see, e.g., Saunders et al., 2012), However, large inter-annual variation in forest C fluxes is common (see, e.g., Allard et al., 2008; Granier et al., 2008; Wilkinson et al., 2012), which makes unequivocal determination of the effect of thinning difficult from short time series. Alternatively, if only a portion of the forest stand is subjected to the thinning, contemporaneous treatment and control plots are possible, and paired EC systems may be used to detect the fluxes from each section (see, e.g., Moreaux et al., 2011), although this approach requires extensive and homogeneous forest areas. For this study, neither of these approaches were available, and so the area and extent of the thinning operation was deliberately manipulated so that the EC tower was sited near the line dividing the treatment and control portions of the forest.

Assessing the impacts of management thinning on the net ecosystem exchange (NEE) of a forest stand is further complicated because NEE is the small difference between ecosystem respiration (R_{eco}) and gross primary productivity (GPP), both of which are much larger components; a small shift in the balance between these will therefore have a large effect on NEE. Furthermore, the ways R_{eco} and GPP are affected by thinning will differ; for example, thinning changes the canopy density, altering the soil temperature and moisture conditions (see, e.g., Tang et al., 2005; Olajuyigbe et al., 2012) and affecting the soil component of R_{eco}. Vesala et al. (2005) found that whilst there was no reduction in the size of the carbon sink of a boreal Scots pine (*Pinus sylvestris* L.) stand in Finland following thinning, increases in ground vegetation photosynthesis and heterotrophic respiration were offset by decreases in canopy GPP and in both above- and below-ground autotrophic respiration. Amiro et al. (2010) published a comprehensive study tracking changes in net ecosystem productivity (NEP) across a variety of different forest types following a range of disturbance events. All three conifer forests studied that were subjected to thinning showed relatively short-term impacts on the carbon balance following a decrease in NEP in the year of disturbance. Other studies in managed forests have shown that NEP rates are sustained following the thinning of canopy trees (e.g. Granier et al., 2008), which is often attributed to increased growth by subcanopy plants after dominant canopy trees have been removed (Moreaux et al., 2011; Dore et al., 2012). Many of these studies are concerned with coniferous forests with very different seasonal dynamics to the deciduous oak woodland found in much of lowland England.

Aerial light detection and ranging (lidar) is a remote sensing method capable of producing three-dimensional models of large areas of landscape with sub-metre accuracy and has been used to measure forest height for more than a decade (see, e.g., Yu et al., 2003). In recent years, its application in forest inventories has become common practice, particularly in northern European countries, where the method is used to quickly cover large areas at a high spatial resolution (Næsset, 2004; Maier et al., 2006). Additionally, the ability to view the resulting data in a variety of ways removes the problems associated with illumination and shadowing seen with standard aerial photography. By carrying out aerial lidar surveys before and after a management thinning operation, it is possible to quantify the changes in the forest canopy structure.

The aim of this study was to examine the effects of management thinning on the factors determining the carbon balance of a plantation deciduous oak woodland in southern England. Our hypotheses were that the removal of preselected trees from the woodland during a thinning operation would lead to an initial reduction in GPP. As thinning also increases the amount of woody debris and other litter components added to the forest floor, an increase in R_{eco} was also expected. Together, these changes would result in a large decrease in NEE during the period immediately after thinning, which would be followed by a recovery of NEE to pre-thinning rates over a period of time, possibly several years, although we could not predict the timescale.

2 Materials and instrumentation

2.1 Site description

The eddy covariance measurement site is located in the Straits Inclosure, Alice Holt Research Forest, UK (51°09′ N; 0°51′ W), close to the Alice Holt Research Station in south-eastern England (Fig. 1a). The inclosure is a flat area with an elevation of 80 m above mean sea level; the surrounding landscape consists of mixed lowland woodland and both arable and pasture agricultural land. The whole 90 ha inclosure was planted in the 1820s with oak (Schlich, 1905) and then replanted in the 1930s. The main tree species is *Quercus robur* L., but other species, including European ash (*Fraxinus excelsior* L.), Q. *petraea* (Mattuschka) Liebl. and *Q. cerris* L., are present. There is a small area (4.6 ha) of mixed conifers consisting of Corsican pine (*Pinus nigra* subsp. *laricio* Maire.) and Scots pine (*Pinus sylvestris* L.) at the north-west edge of the woodland and isolated pockets of Japanese red cedar (*Cryptomeria japonica* (L.f.) D. Don) are also present in the eastern area. The understorey is dominated by hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* Jacq.) (Pitman and Broadmeadow, 2001). Prior to this study, the whole of the stand was previously thinned in 1995.

The climate regime is mild temperate oceanic; the long-term mean (1971–2000) screen annual air temperature was 9.6 °C and the mean annual precipitation 779 mm at the UK Meteorological Office affiliated weather station, Alice Holt, Farnham (51°10′ N, 0°51′ W), approximately 1.8 km from the measurement site. Further site-specific details can be found in Wilkinson et al. (2012).

Between June and August 2007, the eastern half of the woodland (approx. 47.5 ha) was selectively thinned (Fig. 1a)

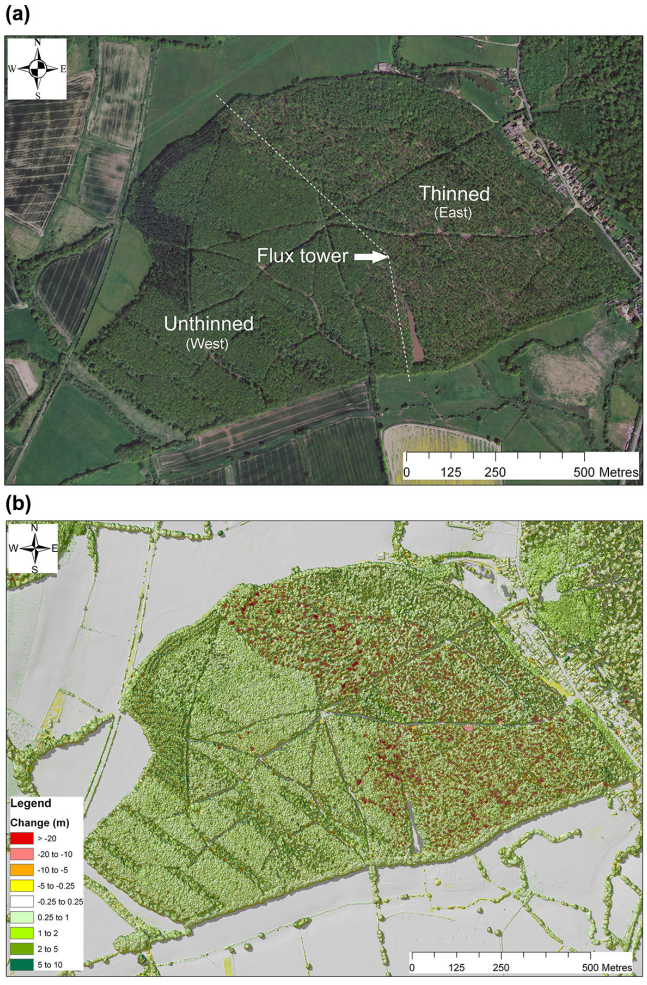

Figure 1. Panel **(a)**: aerial photograph (taken in spring 2008) of the Straits Inclosure, Alice Holt Forest. ©Bluesky International Ltd/Getmapping PLC. Panel **(b)**: change in canopy height between November 2006 and August 2009 calculated using aerial lidar data at the Straits Inclosure, Alice Holt Forest.

using an intermediate thinning procedure (see introduction) resulting in an open forest canopy with a uniform stand structure (Kerr and Haufe, 2011). Preselected trees (based on stem form and position within the canopy) were felled, delimbed and sectioned using mechanical harvesters. The merchantable stem wood with a diameter > 7.0 cm was subsequently collected and transported to the forest roadside using a forwarder, before being removed from the forest by timber haulage lorries. This harvesting technique resulted in substantial disturbance to the understorey and shrub layer. Whilst all of the remaining woody debris was left on the site, some of it was collected and used to construct "brash mats" for machinery movement in order to minimise damage and compaction to the soil, especially in areas of heavy traffic. Mensuration surveys carried out after the thinning in 2009 (western sector) and 2011 (eastern sector) showed 453 and 354 trees ha^{-1} respectively, a difference in stand density of approx. 22 % (Table 1).

2.2 Micrometeorological measurements and flux calculations

Eddy covariance (EC) measurements of energy flux (sensible and latent heat), momentum, net ecosystem exchange (NEE) and water vapour flux have been made above the forest canopy at the site since 1998. The flux tower is located close to the boundary of the thinned and unthinned sectors (Fig. 1a). The EC instrumentation consisted of a three-dimensional sonic anemometer (model Solent R2 until September 2011, model Solent R3 thereafter; Gill Instruments, Lymington, UK) and a closed-path infrared CO_2 and H_2O analyser (model LI-6262 until October 2005, model LI-7000 thereafter; LI-COR Biosciences, Lincoln, Nebraska, USA), sampling air at 28 m height. Raw high-frequency data (20.8 Hz) were logged using the Edisol software package (Moncrieff et al., 1997). Further details of the instrumentation can be found in Wilkinson et al. (2012). For that previous paper, post processing of the raw high-frequency data was performed using the Edinburgh University micrometeorological software tool EdiRe (http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe/); here we used the EddyPro software package (Version 4.2.1, LI-COR Biosciences, Lincoln, Nebraska, USA) but with similar processing options. The angle of attack correction (specific to Gill anemometers) was applied according to Nakai et al. (2006). Double axis rotation tilt correction was also applied to ensure that the vertical velocity signal was orthogonal to the plane of mean air flow. The lag time of the sample from the intake point to the measurement cell of the infrared analyser was determined by maximising the covariance between the vertical wind velocity and scalar concentration. In order to account for flux loss caused by signal damping inside the tube, limited time response and sensor separation, etc., spectral corrections were applied using the fully analytical approach of Moncrieff et al. (1997). Following an analysis of night-time NEE dependence on friction velocity using the method described by Papale et al. (2006), night-time NEE data were rejected where friction velocity was less than a critical threshold (Supplement Table S1). Since CO_2 profile data were not available for the entire measurement period, we have made no corrections for CO_2 storage below the EC instruments. Footprint analysis was performed based on the flux footprint model of Kljun et al. (2004), and the half-hourly flux measurements were rejected when more than 10 % of the measured flux was derived from outside the woodland, our area of interest.

2.3 Flux data processing and treatment separation

Following the calculation of corrected NEE and in order to remove extreme spikes, which were assumed not to be biologically valid, a data filter was applied using an approach

Table 1. Results of tree mensuration surveys carried out in 2009 (west sector) and 2011 (east sector) at the Straits Inclosure, Alice Holt Forest. In the east sector, 26 circular plots were measured, each with a radius of 12.6 m, whilst in the west sector, 18 plots were measured, each with a plot radius of 8 m. Plot locations were selected using a stratified grid basis to ensure the heterogeneity of the forest structure was measured; figures in brackets are standard error.

	All trees		Oak trees only	
	Density (trees ha^{-1})	Mean diameter at breast height (cm)	Density (trees ha^{-1})	Mean diameter at breast height (cm)
East	354	23.9 (0.55)	217	30.0 (0.53)
West	450	26.6 (0.57)	423	26.8 (0.57)

similar to that proposed by Papale et al. (2006) and Thomas et al. (2011). For each calendar year, NEE data were first split into positive or negative values. Positive values more than the mean positive value for the whole year plus 3 standard deviations were removed and the same approach applied to all negative values. A secondary stage data filter was subsequently applied, which removed positive values more than the mean monthly value for that half-hourly period plus 3 standard deviations, and negative values less than the mean monthly value minus 3 standard deviations.

Thirty-minute average flux data (including additional meteorological data such as air temperature, humidity and incident solar radiation (S_g)) were separated into two sectors according to wind direction: data that were collected when the wind direction was between 315 and 170° were classified as "east sector" (the area that was thinned in 2007), and data collected when the wind direction was between 170 and 315° were classified as "west sector" (unthinned area). Table 2 summarises the data availability after this classification into the two sectors. Ecosystem respiration (R_{eco}) was calculated for each sector using the method proposed by Reichstein et al. (2005). Here, each data set was split into 10-day consecutive periods and R_{eco} was estimated using the Lloyd–Taylor regression model (Lloyd and Taylor, 1994) between night-time CO_2 flux (global solar radiation $< 20\,W\,m^{-2}$) and air temperature. The estimated value of R_{eco} was then assigned to the central time point of the averaging interval and linearly interpolated between time points.

2.4 Model parameters

In order to examine changes in the physiological drivers of the carbon balance, original quality-controlled daytime and night-time 30 min average NEE data were separated and analysed independently. The temperature sensitivity of ecosystem respiration for each sector of the forest was determined using an exponential equation fitted to the average half-hourly night-time NEE and air temperature for each corresponding period:

$$R_s = K_1 \exp(K_2 T_{air}), \quad (1)$$

Table 2. Annual eddy covariance CO_2 flux data capture and quality-controlled data availability following de-spiking, footprint and u^* quality checks (QCs) for each sector by time of day (all in percentage) over the period 2004–2012 at the Straits Inclosure, Alice Holt Forest.

Year	Total data capture	QC east day	QC east night	QC west day	QC west night
2004	79.6	8.9	6.1	18.7	14.7
2005	92.5	11.6	8.3	21.6	16.3
2006	74.3	10.7	8.6	16.6	11.4
2007	92.5	9.9	6.3	18.6	12.8
2008	81.4	10.7	6.4	26.0	21.o
2009	77.3	11.9	10.0	15.7	12.9
2010	93.0	15.9	10.5	18.9	14.1
2011	86.7	12.6	9.5	18.4	15.1
2012	82.1	11.9	8.6	18.0	14.9
Mean	84.4	11.6	8.3	19.2	14.8

where R_s is the night-time NEE and T_{air} is the night-time air temperature at 26 m. Data fitted to this function were limited to night-time condition only where the mean half-hourly $S_g < 20\,W\,m^{-2}$ and the quality control flag calculated by EddyPro according to the Mauder and Foken (2006) method was equal to 0.

The relationship between summer (July and August) daytime NEE and S_g was modelled using a rectangular-hyperbolic function:

$$NEE = \left[\frac{(\varepsilon \cdot F^{\infty} \cdot S_g)}{(\varepsilon \cdot S_g + F^{\infty})}\right] + R_d, \quad (2)$$

where F^{∞} is the asymptotic net CO_2 assimilation rate, ε is the initial slope of the light response curve and R_d is respiration in the dark. Data fitted to the light response model were limited to periods where the quality control flag (Mauder and Foken, 2006) was equal to 0.

2.5 Lidar measurements and calculation of vegetation structure

The aerial photograph taken after thinning (Fig. 1a) and mensuration surveys revealed substantial spatial heterogeneity

within the forest block and showed large differences in forest structure between the two sectors. Changes in canopy top height and gap fraction were assessed using aerial lidar surveys conducted over two flight campaigns for the whole of Alice Holt Forest (800 ha) by the Unit for Landscape Modelling (ULM; Dept. of Geography, University of Cambridge). The first was in early November 2006, prior to the thinning, and the second in August 2009, 2 years after the thinning. Due to the mild autumn in 2006, both surveys were completed whilst the forest had a fully developed canopy. A lidar system (ALTM 3033, Optech Incorporated, Ontario, Canada) flown at an altitude of 1000 m above ground level and with a scan angle ±15° was used along a series of overlapping transects designed to cover the whole forest. The system combined a pulse rate of 33 kHz and an overlap of 50 % between swaths, resulting in a point density of 2 to 4 points m^{-2}, which was used to generate a virtual cloud of three-dimensional data points with an accuracy of ±15 cm root mean square (rms). The first- and last-pulse return data were used to generate a digital surface model (DSM) which included the tree cover and a digital terrain model (DTM) representing the ground surface. These data were provided by the ULM as raster elevation models with a 0.5 m cell size. By subtracting the DTM from the DSM using GIS software (ArcGIS 10, Esri, Redlands, California, USA), canopy height models (CHMs) for each survey were created. Furthermore, by subtracting the 2006 DSM from the 2009 DSM, a model of change between the two surveys was also created (Fig. 1b).

To allow a detailed analysis of the vertical change in forest height and gap frequency between 2006 and 2009, each CHM was converted to a 1 m cell size and then spatially split into a 1 ha grid. Canopy top height histograms (bin size: 50 cm) were calculated for each grid cell, based on the 10 000 values per hectare. Frequencies were then averaged for all the grid cells within each sector. Grid cells at the interface between the east and west areas of the forest were excluded from the analysis, as were those cells that contained, either wholly or partially, areas of the surrounding agricultural land. All analyses were conducted using R software (R Development Core Team, 2011).

3 Results

3.1 Climatic conditions

The prevailing wind direction at the site is from the southwest, so more of the data come from periods when the wind is from the west sector (Table 2). As the meteorological conditions associated with easterly and westerly winds differ, the flux data recorded from the two sectors did not reflect the same meteorological conditions (Fig. 2). Mean canopy level annual air temperature (2004–2012) was slightly warmer when air flow was from the west sector (10.8 °C) than from the east sector (9.6 °C).

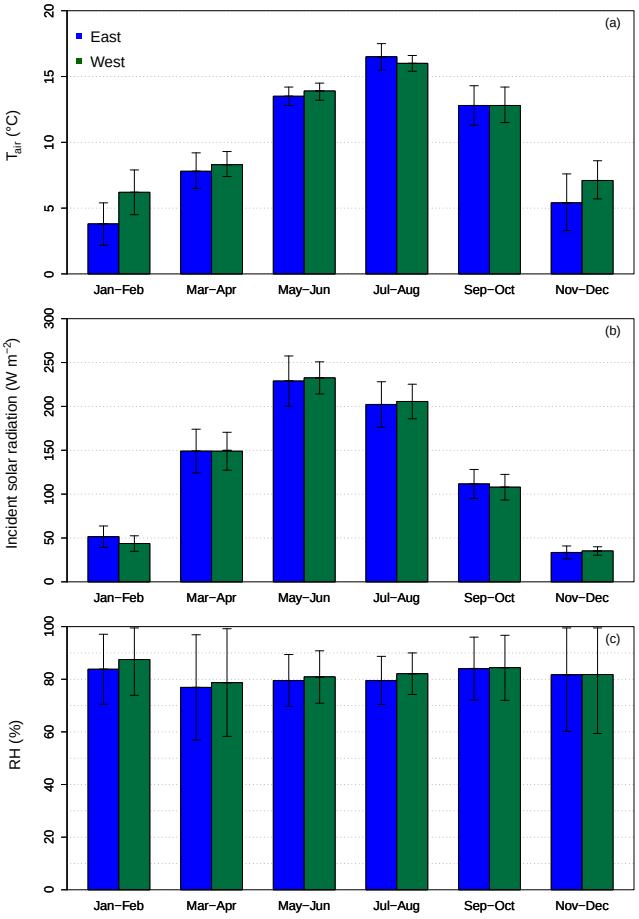

Figure 2. Average bimonthly values (2004–2012) for the key climatic variables of **(a)** air temperature, **(b)** incident solar radiation, S_g, and **(c)** relative humidity for the east (blue) and west (green) sectors (error bars represent ±1 standard deviation; $n = 7$) at the Straits Inclosure, Alice Holt Forest.

The mean diurnal course of air temperature over the bimonthly winter periods of November–December and January–February was generally warmer when airflow was from the more usual west rather than the east. The largest difference in winter air temperature was observed in January–February 2012: a period of cold weather from the start of February, dominated by easterly conditions, persisted over the southern UK for about 2 weeks and was also associated with snowfall in parts of the region (Fig. 3a). Conversely, mean summer air temperatures (during daylight hours) were generally higher when airflow was from the east than from the west, as occurred in 2004. Incident solar radiation and relative humidity were generally very similar when air flow was from either sector (Fig. 2).

3.2 Variation in NEE

The mean diurnal course of NEE (Fig. 3b) indicated that the forest generally acted as a CO_2 source for the bimonthly peri-

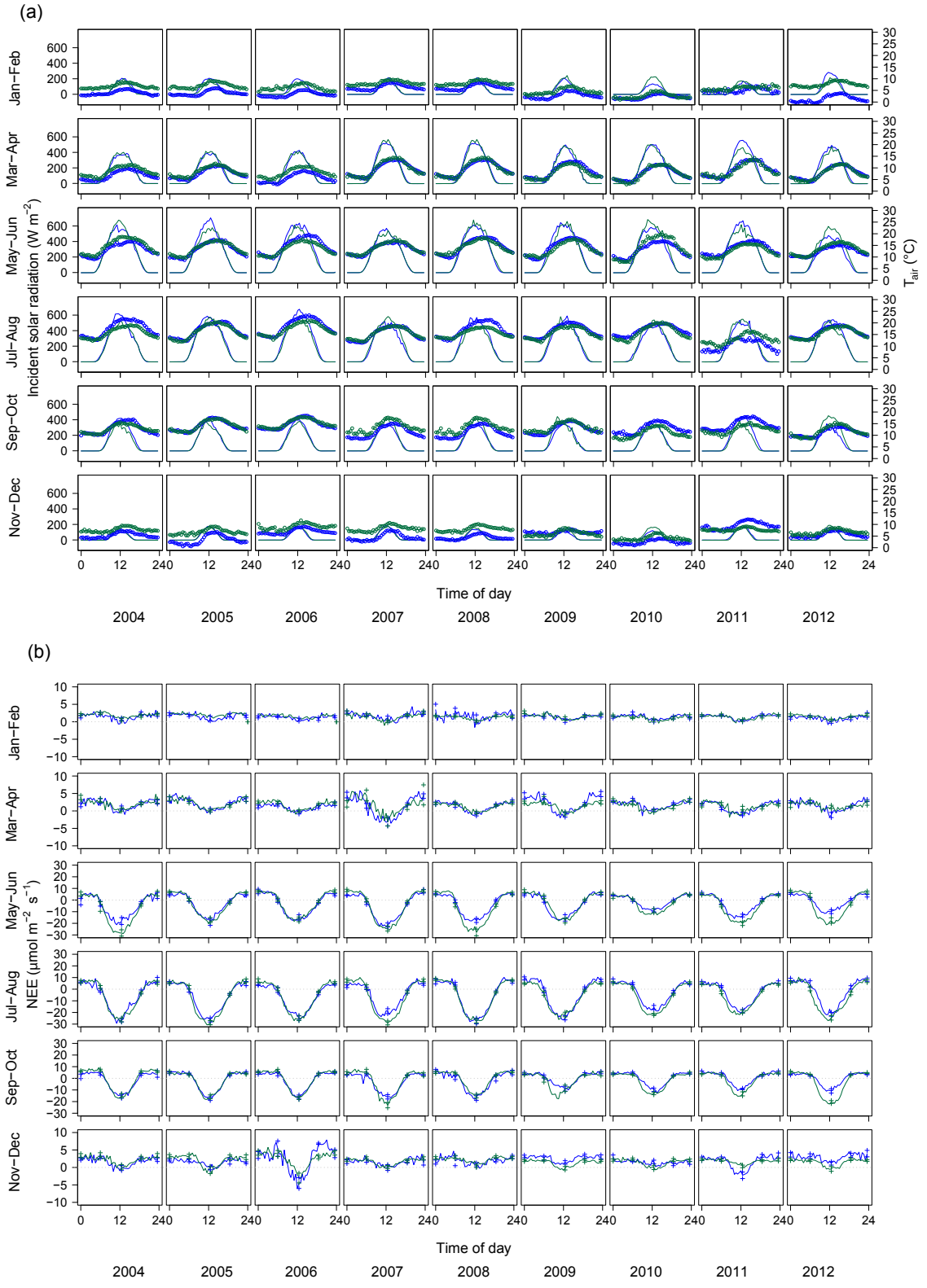

Figure 3. Panel **(a)**: average bimonthly diurnal curve of incident solar radiation, S_g, for east sector (blue solid line) and west sector (green solid line) and air temperature for east sector (blue open circles) and west sector (green open circles) for 2004, 2007 and 2012 at the Straits Inclosure, Alice Holt Forest. Panel **(b)**: mean bimonthly diurnal curve of net ecosystem exchange for east sector (blue solid line) and west sector (green solid line) for 2004, 2007 and 2012; + symbols represent ±1SE at the Straits Inclosure, Alice Holt Forest.

ods of November–December, January–February and March–April, although in exceptionally warm and early springs, such as 2007, the forest became a weak CO_2 sink for a few hours around noon. Both sectors of the forest were a strong CO_2 sink from May through to October, although there was considerable variation between years. In some periods, when temperature and insolation conditions were very similar for each sector, NEE patterns were also similar (e.g. May–June 2007 and March–April 2012). In other periods with similar temperature and insolation, NEE was different, for example, in July–August 2012.

3.3 Effects of thinning on ecosystem respiration

As expected for a temperate, deciduous forest, there was a large annual cycle in R_{eco}, with a peak in May–August (Fig. 4a–c) but varying substantially year to year. Before thinning, annual R_{eco} patterns were similar between sectors (e.g. Fig. 4a, 2006), but in the immediate period after thinning, R_{eco} was usually higher in the east sector (e.g. Fig. 4b, 2009), particularly in the warmer summer period. As weather conditions differed for fluxes measured for east and west, we compared the underlying relationships of R_{eco} with temperature between sectors.

As an assessment of the sensitivity of R_s to air temperature, using the coefficients of the exponential function (Eq. 1) revealed differences between sectors (Table 3). Overall Q_{10} was generally higher and more variable between years, when airflow was from the west sector (mean: 2.92; SD: 0.74) than from the east (mean: 2.08; SD: 0.23); however, this was not the case in 2009 and 2010. The largest differences in R_s (highest in the east) between the two sectors occurred in 2009, 2 years after the thinning. This was the only year during which there was a constant small (although non-significant) positive offset in the sensitivity of R_s to air temperature between the two sectors (Fig. 4h).

3.4 Effects of thinning on canopy NEE light response

The asymptotic net CO_2 assimilation rate (F^{∞}) and apparent quantum yield (ε) were determined from a light response function (Eq. 2) fitted to the summer (July and August) daytime NEE flux data for both forest sectors. Differences in F^{∞} were observed between the east and west sectors both before and after thinning (data not shown). Although both sectors followed the same general inter-annual pattern, there was no clear change (in either sector) after thinning. The magnitude of F^{∞} was generally larger than the maximum observed rates of daytime NEE, due to an overestimation of F^{∞} by the rectangular-hyperbolic model; therefore, NEE at S_g 800 Wm^{-2} (NEE_{800}) was considered a better indication of the maximum rate of light-saturated NEE. NEE_{800} was consistently lower in the fluxes observed from the east sector (Fig. 5a) than from the west for the entire measurement period; there was no significant reduction in NEE_{800} in 2008 in fluxes from either sector. Prior to 2007, the magnitude of apparent quantum yield (Fig. 5b) was generally higher when fluxes were from the west than from the east; the two sectors converged in the post-thinning phase. R_d (respiration in the dark) estimated from the light response curves increased in the east sector post thinning relative to the west and remained higher through to 2012 (Fig. 5c) confirming the results of R_{eco} estimated using the Reichstein et al. (2005) method.

3.5 Changes in canopy height and gap fraction

The canopy top height derived from the first-return data from the lidar survey showed that the two sectors of forest had similar canopy height distributions in 2006, before thinning (Fig. 6a, b), but with some differences in detail. The small peak in frequency between 5 and 10 m height in the west in 2006 (Fig. 6a) is from areas of the forest which were undergoing succession development following previous disturbance events. By 2009 these areas of the forest had grown and are evident as heterogeneous patches in Fig. 1b. In both sectors, the canopy height distribution profile changed, in the west this was because of growth, whilst in the east the thinning operation had a substantial effect. Prior to the thinning, both maximum and mean canopy heights were similar in both sectors (Table 4). Between 2006 and 2009, the maximum canopy height increased in the west sector by 0.9 m but was reduced slightly in the east sector by 0.1 m. Over the same time period, mean canopy top height also increased in the west sector by 0.95 m and reduced in the east sector by 1.4 m.

Changes in the canopy height distribution profiles were also observed (Fig. 6c, d). The elevation relief ratio, E (Pike and Wilson, 1971), reflects the degree to which the outer canopy surfaces are in the upper ($E > 0.5$) or lower ($E < 0.5$) portion of the height range and is defined as

$$E = \frac{h_{mean} - h_{min}}{h_{max} - h_{min}}, \quad (3)$$

where h_{mean}, h_{min} and h_{max} are the mean, minimum and maximum canopy heights respectively. E was reduced substantially in the east because of the larger proportion of lower top heights, while there was only a small increase in E in the west (Table 4). The canopy top height distribution also showed a relatively small increase in the proportion of canopy > 15 m in height between 2006 and 2009 in the west (+6.2 %) but a substantial reduction in the east (−13.7 %) as a result of the thinning operation.

The lidar survey also showed that canopy complexity across the uppermost surface of the forest in the east sector increased following the thinning operations. The relative variability in canopy height (indicated by the coefficient of variation) increased substantially (Table 4) in the east but not in the west. After thinning there was a large increase in the frequency of gaps in the forest canopy (canopy top height < 1 m) in the east sector but not the west because of the re-

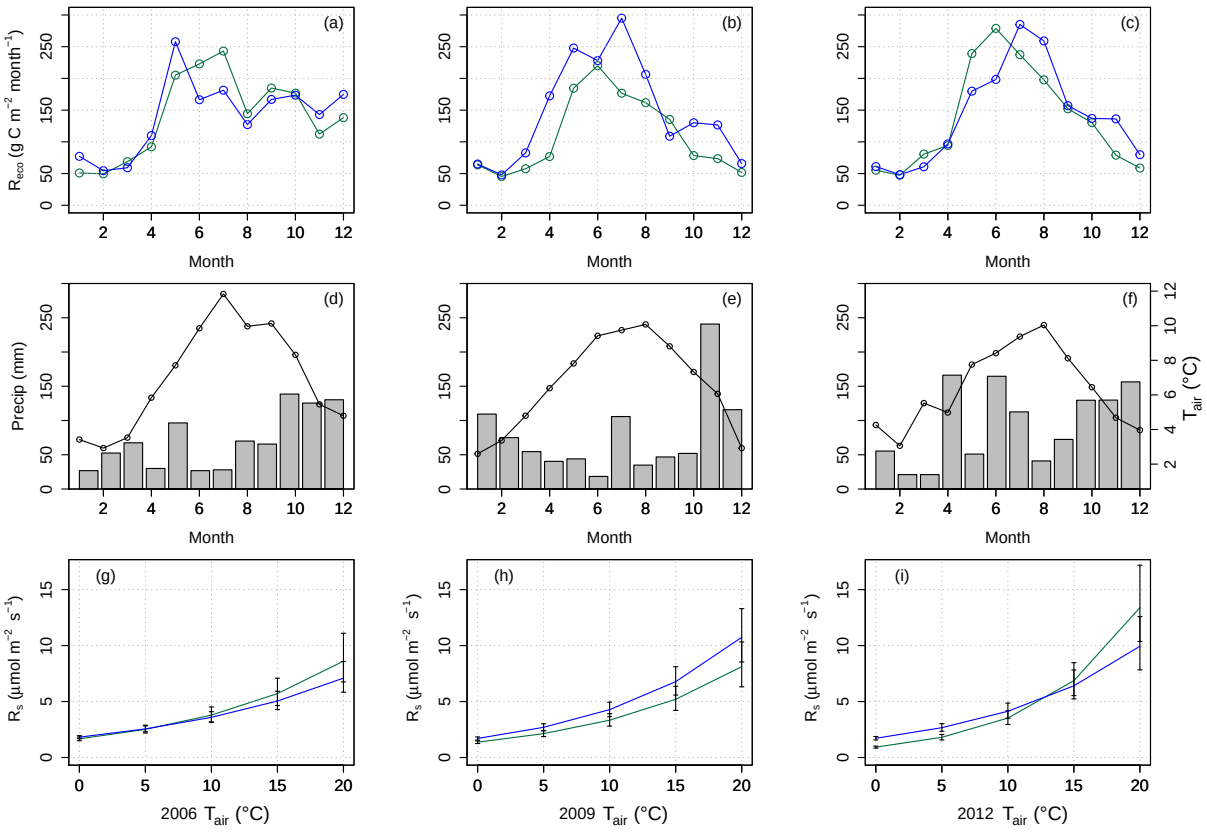

Figure 4. Monthly estimated R_{eco} for the east sector (blue solid line with open circles) and west sector (green solid line with open circles) for **(a)** 2006, **(b)** 2009 and **(c)** 2012; monthly mean air temperature (at 26 m height) and monthly precipitation total for **(d)** 2006, **(e)** 2009 and **(f)** 2012; modelled temperature response (R_s derived from night-time NEE fluxes only) for east sector (blue sold line) and west sector (green solid line) for **(g)** 2006, **(h)** 2009 and **(i)** 2012 (error bars represent 95 % confidence intervals) at the Straits Inclosure, Alice Holt Forest.

Table 3. Night-time ecosystem respiration (R_S) coefficients and the estimated Q_{10} values (base temperature: 0 °C) derived from fitting an exponential equation to half-hourly night-time NEE and air temperature values over the period 2004–2012 at the Straits Inclosure, Alice Holt Forest.

Year	K1 east	K2 east	K1 west	K2 west	Q_{10} east	Q_{10} west
2004	2.22 (0.07)	0.064 (0.003)	1.22 (0.06)	0.120 (0.003)	1.90	3.32
2005	2.14 (0.06)	0.063 (0.002)	1.59 (0.07)	0.091 (0.003)	1.88	2.48
2006	1.82 (0.07)	0.068 (0.003)	1.67 (0.08)	0.082 (0.003)	1.97	2.27
2007	2.08 (0.10)	0.061 (0.004)	1.11 (0.06)	0.122 (0.004)	1.84	3.39
2008	1.82 (0.07)	0.078 (0.003)	0.81 (0.04)	0.140 (0.003)	2.18	4.06
2009	1.71 (0.07)	0.089 (0.003)	1.37 (0.06)	0.089 (0.089)	2.44	2.44
2010	1.70 (0.05)	0.072 (0.002)	1.74 (0.05)	0.064 (0.002)	2.05	1.90
2011	1.62 (0.08)	0.071 (0.004)	1.15 (0.05)	0.098 (0.004)	2.03	2.66
2012	1.72 (0.08)	0.088 (0.004)	0.93 (0.05)	0.134 (0.004)	2.41	3.82

Figures in brackets are 1 standard error (SE).

moval of canopy trees (compare Fig. 6d). Gaps in the forest canopy were relatively uniformly distributed throughout the whole east sector and increased from a total area of 1.13 ha (3.1 % of the eastern area) in 2006 to 2.16 ha (6.6 %) in 2009. Over the same period there was a small decrease in the total area of gaps in the forest canopy in the west, which measured 0.89 ha (2.47 % of the total western area) in 2006 and 0.85 ha (2.35 %) in the 2009 surveys (Fig. 1b).

Table 4. Results of aerial lidar surveys before and after thinning calculated from first- and last-return data at a point density of 2 points m^{-2} and extracted from a 1 ha gridded canopy height model at the Straits Inclosure, Alice Holt Forest. C.V.: coefficient of variation.

Year	Sector	Maximum height (m)	Mean height (m)	SD of mean height	C.V.	Elevation relief ratio (E)	% of canopy > 10 m	% of canopy > 15 m
2006	West	25.7	15.0	5.04	0.34	0.58	81.9	66.3
2006	East	26.0	15.0	5.03	0.34	0.57	84.5	65.3
2009	West	26.6	15.9	4.99	0.32	0.59	85.8	72.5
2009	East	25.9	13.6	6.19	0.46	0.52	73.6	51.7

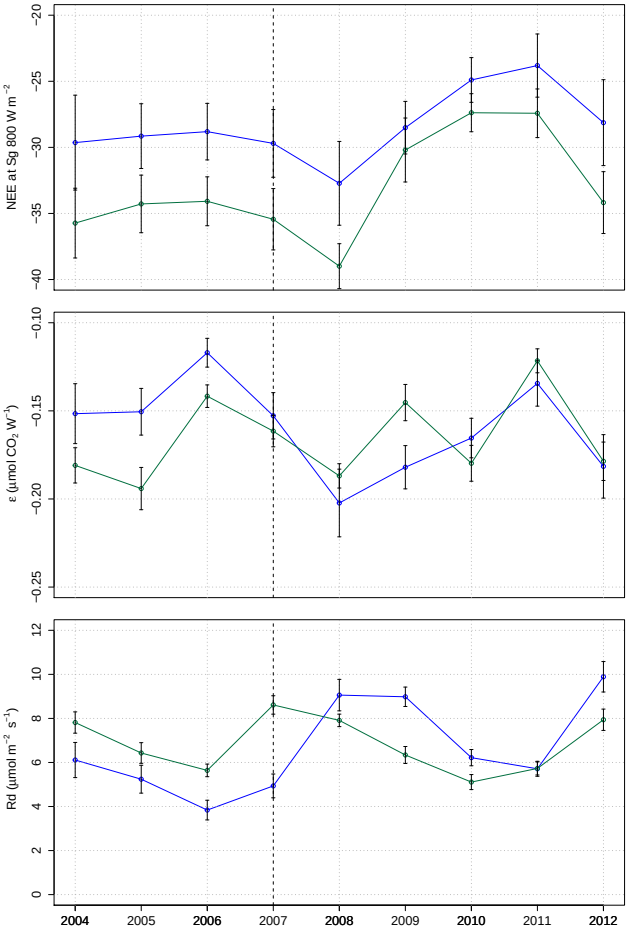

Figure 5. Inter-annual variation in summer (July and August) daytime light response model parameters for **(a)** NEE_{800}, **(b)** ε and **(c)** R_d for the east sector (blue line with open circles) and west sector (green line with open circles), with error bars representing ±1SE, at the Straits Inclosure, Alice Holt Forest.

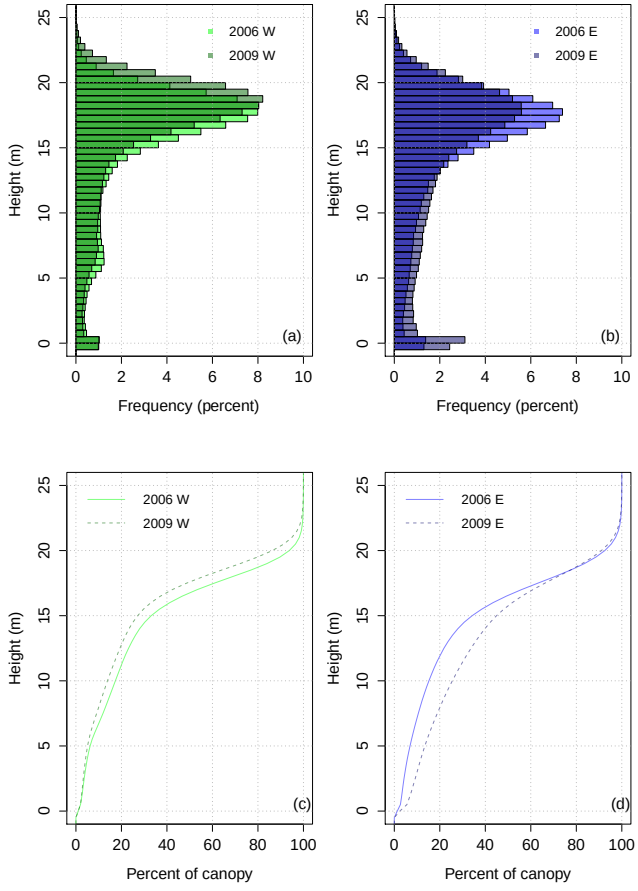

Figure 6. Histograms of canopy top height (m) derived from aerial lidar for the east sector (blue bars) and west (green bars) for **(a, b)** 2006 and 2009; cumulative frequency of canopy top height for **(c)** west sector in 2006 and 2009 and **(d)** east sector in 2006 and 2009 at the Straits Inclosure, Alice Holt Forest.

4 Discussion

Surprisingly, the effects of the thinning procedure in 2007 on the carbon balance were not clearly evident. In part, this may have been because of our experimental approach. We used eddy covariance measurements at one location near the boundary between the thinned and unthinned sectors in order to determine the CO_2 fluxes because of the relatively small size of the forest block and being restricted to only one tower and EC system. The effects of thinning are partly obscured by (a) the differences in weather conditions when airflow is from either sector (Fig. 2), (b) existing heterogeneity in fluxes from different parts of the forest prior to thinning (Fig. 3b) and (d) the limited data availability for each sector (Table 2).

The pre- and post-thinning lidar surveys indicated that whilst canopy top height distributions were comparable in 2006, the thinning operations in 2007 had a large effect on the canopy structure of the east sector, resulting in a more complex canopy with a wider range of top heights and a larger total area of gaps. The complexity of the forest canopy at our site, as a result of variability in gaps and a dense understorey, contrasts with other published studies using lidar at other deciduous forest sites (Wasser et al., 2013). Whilst we acknowledge that the 2009 lidar survey did not take place immediately after the thinning, our estimate of the change in canopy gap fraction may be an underrepresentation. Firstly, lidar pulses have a relatively large footprint (~ 25 cm in diameter) and therefore gaps in the canopy would need to be larger than this in order to be recognised as a gap. Secondly, off-nadir pulses are more likely to produce a canopy height return than they are to penetrate to ground level. Our approach used only the first- and last-return signals of the lidar data, so the canopy height model showed only the uppermost component of the forest canopy. As such, some of the changes in the understorey canopy during thinning may have been masked by the vertical overlap of the understorey vegetation and upper canopy. Whilst we acknowledge that an analysis of full waveform or multiple return data (Mallet and Bretar, 2009) may provide more detailed information about the canopy's three-dimensional structure, we maintain that the approach adopted here provided a useful assessment of the changes to the forest canopy due to the thinning operations.

The parameters obtained from the summer light response curves did not support our hypothesis that tree thinning would lead to a reduction in NEE through a loss of canopy photosynthetic area. Contrary to expectation, there was no clear difference in NEE_{800} (Fig. 5) in 2008 for the east sector relative to the west. We suggest that this apparent insensitivity in 2008 to the thinning indicates that in the first year after thinning the newly exposed ground vegetation and shrub layer and better illumination of the remaining crowns compensates for the removed trees. From 2009 to 2011, NEE_{800} was reduced in both sectors probably as a result of defoliation by caterpillars (Wilkinson et al., 2012). The increase in ε in the east in 2008 and especially 2009 may be as a result of the thinning as it consistent with the earlier work of Niinemets (2007) and Pangle et al. (2009), who demonstrated that as forest canopies become more structurally diverse, light efficiency increases because of a more even distribution of radiation throughout the tree canopy and better light penetration to subcanopy species with a higher ε. Our findings however contrast with results from thinning studies carried out on evergreen conifer sites (with presumably little or no understorey vegetation). For example, Saunders et al. (2012) attributed observed changes in the photosynthetic efficiency of a Sitka spruce stand following thinning to inherent change in the photosynthetic efficiency of the remaining trees rather than to increased light absorption.

The impacts of thinning on respiration are complicated by the fact that R_{eco} consists of CO_2 derived from both heterotrophic respiration (R_h) largely in the soil and from autotrophic respiration (R_a), both above and below ground. Both of these CO_2 sources comprise a number of processes and components which are likely to be influenced by both time and forest management in different ways. R_d estimated from the light response curves increased in the first years after thinning in the east relative to the west. In the first years after thinning (2008–2010) the initial supply of fine roots, small twigs, leaves and other easily degradable fractions of litter would be a major new source of carbon and nitrogen for the decomposition system. Soil disturbance from machinery might also be expected to increase R_h as was demonstrated by Concilio et al. (2009) at a mixed species conifer site. In addition, much of the large woody debris had been gathered together to form brash mats which may have been a substantial source of CO_2, although we have no independent measurements of emission from them. Thinning is also likely to cause local increases in temperature, increased throughfall, reductions in humidity and probably higher evaporation rates in gaps (Vesala et al., 2005). However, we cannot quantify such effects as the climatic data we recorded were only that from the central instrument tower. After thinning there is likely to be a succession of changes in the relative contributions of R_a and R_h to total R_{eco}, which may be associated not only with changes to soil conditions but also with biomass removal (Anderson-Teixeira et al., 2011) and a reduction in GPP (Woodward et al., 2010). Although we do not have independent measures for R_a and R_h throughout the period of the present study, work at the site in 2008–2010 (Heinemeyer et al., 2012) demonstrated that in an unthinned area the largest proportion of total soil efflux was from R_a (56 %) compared with R_h (44 %). Importantly for this study, Heinemeyer et al. (2012) demonstrated a stronger temperature response for R_h than for either root R_a or mycorrhizal R_a. After thinning the proportion of total soil CO_2 efflux derived from R_h is likely to increase, which may result in an increased temperature sensitivity of CO_2 efflux by forest soils. In 2011 there was no clearly discernable difference in R_{eco} between the two sectors, and we therefore assume that any increase in below ground R_h is likely to be cancelled out by a corresponding reduction in R_a, which is consistent with the findings of Tang et al. (2005).

In a previous paper describing the pattern of CO_2 fluxes at this site between 1999 and 2010 (Wilkinson et al., 2012), we noted the substantial inter-annual variation in NEE. The analysis presented here (e.g. in Fig. 3) suggests that part of this may be caused by inter-annual differences in the contribution from the east and west areas of the forest, which differed even before the thinning.

5 Conclusion

This study has investigated the effects of management thinning on the carbon balance of deciduous oak woodland in south-eastern England. Lidar data were used to assess changes in the forest canopy, while EC was used to measure changes in the carbon balance. Management thinning reduced the mean canopy top height and resulted in a forest canopy with a wider top height range and more gaps. The impacts of management thinning on the carbon balance were not clearly evident although ecosystem respiration was higher in fluxes from the east sector from 2008 onwards and remained higher until the end of the study period. The insensitivity of the summer photosynthetic parameters in the first year after thinning, 2008, suggests that newly exposed ground vegetation and shrub layers receiving better illumination compensated for the removed trees.

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Chapter 4 - Variation in the date of budburst in *Quercus robur* and *Q. petraea* across a range of provenances grown in Southern England

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ORIGINAL PAPER

Variation in the date of budburst in *Quercus robur* and *Q. petraea* across a range of provenances grown in Southern England

M. Wilkinson[1] · E. L. Eaton[1] · J. I. L. Morison[1]

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Abstract The widely observed advance in spring budburst across a range of temperate forest species due to climatic warming has received considerable attention. This change in forest phenology has important implications for the choice of species and provenances currently being planted, which need to be suited to both current and future climatic conditions. Using a provenance trial in the south of England, this study assessed variation in the timing of budburst across 23 different European provenances of oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) over 8 years of observations. The order in which the different provenances reached budburst was related to provenance source latitude: the southern provenances were always earlier than those from more northerly latitudes. The statistical technique partial least squares regression was used to identify critical periods of both chilling and warming. A General Linear Model and three-dimensional temperature response surfaces were used to analyse the temporal trends in budburst. There was a negative correlation between the date of budburst and mean daily air temperature in both the chilling and warming periods for all provenances, which was statistically significant for a majority. Spring warming had a larger effect on budburst than winter chilling with a mean spring temperature-driven advance of 3.61 days/°C (standard error = 0.17 days/°C) and mean winter period temperature-driven advance of 0.99 days/°C (standard error = 0.17 days/°C). Surprisingly, there was no statistically significant interaction between mean air temperatures during the chilling and warming phases on the date of budburst.

Keywords Phenology · Climate change · Oak · Budburst · Provenance

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✉ M. Wilkinson
matthew.wilkinson@forestry.gsi.gov.uk

[1] Centre for Sustainable Forestry and Climate Change, Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK

Introduction

There is substantial evidence that recent climatic warming has had a significant influence on the phenological development of natural and managed ecosystems (Settele et al. 2014). Phenological investigations from both Europe (e.g. Sparks and Carey 1995; Sparks et al. 1997; Menzel et al. 2006; Parmesan 2007; Fu et al. 2014) and North America (e.g. Richardson et al. 2006) have demonstrated advances in spring leaf unfolding and flowering in woody plants in response to climatic warming. Concurrent with shifts in phenology, the risk to trees from encountering cold-related damage at vulnerable periods in their growth cycle is also changing (Vitasse et al. 2014). Whilst the overall impacts of a changing climate on the forestry sector have received considerable attention (e.g. Ray et al. 2010; Kirilenko and Sedjo 2007; Read et al. 2009; Lindner et al. 2014), there is a need for more specific information on the growth, survival and phenological responses of both recently introduced species and of different provenances of native species. This is especially important given the interest of the forestry sector in their potential use as a climate change adaptation measure (Ray et al. 2010). In Britain, there is a long history of provenance trials (Lines 1992; Worrell 1992; Hubert 2005) which were originally established for tree and timber improvement studies and now provide an opportunity to assess the suitability of different tree provenances in the light of climate change.

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Surprisingly, relatively little is known about the differences in phenological sensitivity to temperature between tree species and between populations within a species (Vitasse et al. 2009). This may in part be due to the fact that observational studies (e.g. Wesolowski and Rowiński 2006) require several years of measurements to yield meaningful results and rely on natural climatic variation during the observation period. Alternative methods have been used to examine changing phenological responses include satellite remote sensing (e.g. White et al. 2014; Wang et al. 2015), webcam digital images (e.g. Mizunuma et al. 2012) and experimental warming (e.g. Wolkovich et al. 2012), but these approaches are not well suited for assessing individual tree responses or variations between provenances. Experimental and observational work to examine the phenological response of different provenances of oak (*Q. robur* and *Q. petraea*) from different latitudes has provided contradictory evidence. Earlier budburst of southern provenances in young trees has been reported in some studies (e.g. Liepe 1993; Deans and Harvey 1995; Reid 2011) as has the opposite response (e.g. Jensen and Hansen 2008). Whilst earlier budburst might lengthen the growing season and increase productivity, it can also increase the risk of spring frost damage (Liepe 1993).

In this study, variation in the date of budburst across a range of provenances of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. was examined over 8 years (2004–2010 and again in 2013) using a trial in the south of the England. Importantly, these assessments were made on semi-mature trees (14 years old at start of the study) which had reached a closed canopy state. By carrying out the study at a single site, we avoided any photoperiod effect which can influence phenological studies along latitudinal gradients where temperature and photoperiod co-vary.

The timing of spring phenology such as budburst and leaf unfolding in a majority of temperate plants has long been associated with two distinct temperature-driven processes. Following leaf fall in autumn, a period of cold temperature during which chilling is accumulated is required for the completion of endodormancy; this is followed by a period of warming required for bud and subsequently leaf development. Partial least squares regression (PLS) has recently been used to identify these critical periods of temperature sensitivity using several different long-term phenological data sets (e.g. Luedeling et al. 2009a, b; Luedeling and Gassner 2012; Guo et al. 2015). An objective of this study was to use PLS to determine how air temperature during the chilling and warming periods affected budburst of 23 provenances of oak originating from different source latitudes grown at a single location.

Materials and methods

Study site

Oak budburst phenology was recorded at a forest trial site near Chiddingfold, West Sussex in southern England (51° 06′N, 0°35′W). The trial is one of a series of eight sites in the UK, planted in 1990 and comprises 23 different European provenances (Table 1) of oak *Q. robur* and *Q. petraea*. The provenances originated from a wide latitudinal range (44.42°N–53.13°N) and came from countries including England, France, Germany, the Netherlands, Ireland and Wales. The trial is laid out in a randomised complete block design with three replicate blocks: each block contains one plot of each provenance in a 6 × 6 grid, giving a total of 36 trees per plot for each provenance. The trial site is a flat area with an elevation of 50 m above sea level (asl); the surrounding landscape consists of mixed broadleaf forest, pasture and arable land. At the start of the monitoring period, the mean tree height was ~4.5 m. Earlier results focusing on provenance selection for timber growth properties from this, and other comparable trial sites were published by Hubert (2005).

The climate of the region is temperate oceanic with a long-term (1971–2000) average screen air temperature of 9.6 °C and a mean annual precipitation of 779 mm (long-term climate data derived from the UK Meteorological Office climatological station located at the Alice Holt Research Station, Farnham, UK (51°10′N, 0°51′W) approximately 19 km west of the site). Mean summer (June, July and August) and winter (December, January and February) air temperatures over the period relevant to this study (2003–2013) were 16.6 and 5.1 °C, respectively. The soil is classified as a stagnogley and was derived from the sedimentary rocks of the Wealden Beds.

Phenological observations

The date of budburst was recorded over seven consecutive years (2004–2010) and also in 2013, which had a mean spring (February, March and April) air temperature 1.1 °C cooler than the long-term (1971–2000) average for this site. In each year, the trial was assessed every 2–3 days from early April until all the monitored trees had reached budburst. To avoid any potential bias, observations were always made by the same experienced recorder. At each visit, an assessment was made of the development state of each of the four central trees in each plot, from bud dormancy through to the completion of budburst, using optical binoculars (Prinz 7 × 50) at an approximate distance of ten metres. Assessments were always made in the same region of the upper crowns, from the southern side of the trees and

Table 1 Provenance source region (most northerly first), country, latitude, longitude, altitude (where available), trial code, mean budburst day of year (DOY), standard error (SE) and species for 23 oak provenances at the Chiddingfold phenology trial, West Sussex

Provenance source	Country	Latitude (°N)	Longitude (°E)	Altitude	Code	Mean budburst (DOY ± SE)	Species
Delgany, Wicklow	Ireland	53.13	−6.13	120	De	115 ± 1.71	*Q. petraea*
Coolgreaney, Wexford	Ireland	52.76	−6.25	100	Co	115 ± 1.86	*Q. petraea*
Killarney, Co. Kerry	Ireland	51.97	−9.60	50	Ki	116 ± 2.10	*Q. petraea*
Wienhousen, Lower Saxony	Germany	52.62	10.08	40	We	116 ± 2.37	*Q. robur*
Piene, Lower Saxony	Germany	52.40	10.23	80	Pi	118 ± 1.94	*Q. robur*
Fallersleben, Lower Saxony	Germany	52.37	10.72	70	Fa	119 ± 2.23	*Q. robur*
NL3, Noord-Brabant	Netherlands	51.50	5.70	NA	NL3	120 ± 2.40	*Q. robur*
Brecon, Powys	Wales	52.15	−3.43	150	Br	119 ± 2.28	*Q. robur*
Blakeney, Gloucestershire	England	51.78	−2.50	76	Bl	114 ± 2.15	*Q. robur*
Dymock, Gloucestershire	England	51.95	−2.45	70	Dy	117 ± 2.07	*Q. petraea*
Sutton Bottom, Gloucestershire	England	51.81	−2.49	120	Sb	115 ± 2.03	*Q. robur*
Chiddingfold, Surrey[a]	England	51.10	−0.57	45	Wd	119 ± 2.34	*Q. petraea*
Vinney, New Forest, Hampshire	England	50.85	−1.63	30	Vi	118 ± 2.14	*Q. petraea*
Hurst Hill, New Forest, Hampshire	England	50.84	−1.59	17	Hh	117 ± 2.60	*Q. robur*
South Oakley, New Forest, Hampshire	England	50.84	−1.70	50	So	116 ± 2.26	*Q. petraea*
Nord-Est Limons et Argilles, Lorraine	France	48.80	6.70	325	No	111 ± 1.86	*Q. petraea*
Orleans, Centre-Val de Loire	France	48.00	2.23	137	Or	112 ± 1.98	*Q. petraea*
Berce, Pays de Loire	France	47.79	0.33	155	Be	108 ± 1.64	*Q. petraea*
Basin Superiore de la Saone, Franche-Comté	France	47.50	5.50	NA	Ba	111 ± 2.16	*Q. petraea*
Prémery, Bourgogne	France	47.17	3.33	300	Pr	115 ± 1.93	*Q. petraea*
Charentes Poitou	France	46.62	0.47	115	Ch1	112 ± 1.99	*Q. petraea*
Charentes Poitou	France	46.61	0.70	140	Ch2	111 ± 1.91	*Q. petraea*
Gresigne, Midi-Pyrenées	France	44.42	1.75	305	Gr	110 ± 2.13	*Q. petraea*

[a] Local provenance

at the same time of day. In plots where one of the four central trees was missing, its nearest immediate neighbour was assessed instead. The same trees were used in each plot throughout the whole study. Budburst was considered to have occurred when the first green leaf material was distinguishable from the swelling bud on at least one branch per tree according to the ICP protocol (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests, Manual Part IX Phenological Observations http://www.metla.fi/eu/icp/phenology/). After each individual tree had reached budburst, further observations on it were discontinued for that year.

Climatic data

The nearest long-term daily weather record is at Alice Holt Research Station. In order to check the appropriateness of these data for the trial site, between November 2006 and March 2008 air temperature was measured at the trial site every 30 min using an unscreened temperature data logger (Tinytag model TGP-4017, Gemini Data Loggers, Chichester, UK) mounted on a wooden post, located under the tree canopy at a height of 1.5 m. These data were compared to the screen air temperature (over grass) from an automatic weather station at Alice Holt. Linear regression analysis indicated a very close agreement in air temperatures at the two sites (slope = 1.02, intercept = −0.84 °C, $r^2 = 0.92$, $p < 0.001$) suggesting Chiddingfold was approximately 0.6 °C cooler than Alice Holt in that period. Given this close agreement and because both the phenology trial site and the weather station site are at similar altitudes (~50 m asl) and both are located in rural areas, the hourly mean air temperature from the Alice Holt site was used for all subsequent analysis. The resulting hourly air temperature data were used to calculate continuous winter chill and heat accumulation over the entire measurement period. For both the chill and heat quantification, we followed a procedure similar to that detailed in Luedeling et al. (2013a, b). For chill quantification, we used the Dynamic Model (Erez et al. 1990; Fishman et al. 1987a, b). In this model winter, chilling is assumed to accumulate in a two-step process. At the start of the

relevant period, cold temperatures result in formation of an intermediate chilling product which can be destroyed by high temperatures. Following the accumulation of a critical amount of chilling product, it is converted to a chill portion, which cannot be destroyed. For heat quantification, we used the Growing Degree Hours (GDH) approach by Anderson et al. (1986), and the equations for this model are reproduced in Luedeling et al. (2009a, b). In summary, this model calculates GDH from hourly temperature data as a function of base, optimum and critical temperatures. In order to ensure that recognisable patterns are produced by the PLS analysis (Luedeling and Gassner 2012), both the continuous chill and heat accumulation records were smoothed by applying a 15-day running mean function (Luedeling et al. 2013a, b). All hourly chill and heat data were subsequently assigned to phenological years which for oak trees we defined as starting on the 1 June through to the 31 May in the following year.

Variation in budburst date with source latitude, altitude, continentality and year

The effects of source latitude, altitude, continentality which describes the annual range in monthly mean temperature (Conrad 1946) and year on budburst date were examined using a General Linear Model (GLM) approach. All possible combinations of these four factors were initially included in the various models apart from altitude x latitude x continentality interactions which were excluded because each combination of these is unique to an individual provenance and therefore interactions are not possible. The various model combinations tested were as follows: (a) all combinations of altitude, latitude, continentality and year, (b) all combinations of latitude, continentality and year, (c) all combinations of altitude, latitude and year, and (d) all combinations of latitude and year. The best model in each group was selected (based on deviance), and these four models were then compared sequentially. Data relating to the best fit GLM (budburst, source latitude and year) did not deviate significantly from normal (Shapiro–Wilk normality test, $p = 0.38$).

Identification of relevant periods influencing oak budburst

The critical time periods of chill and heat accumulation during which budburst was sensitive to air temperature were derived using PLS regression. This technique is commonly used in chemometrics (Wold et al. 2001) and also in hyperspectral remote sensing (Luedeling et al. 2009a, b) and is gaining popularity in the analysis of phenological data sets (e.g. Luedeling et al. 2009a, b; Luedeling and Gassner 2012; Guo et al. 2015). PLS regression can be used in situations where independent variables are highly auto-correlated and where the number of independent variables exceeds the number of observations, hence why it is particularly suited to the analysis of phenological data. In this study, the independent variables were daily chill or heat values and the dependent variables were mean annual date of budburst for each provenance. The resulting data set therefore consisted of 365 daily chill values (in leap years, the 31 December was ignored), 365 daily heat values and one budburst date for each year of the study.

The two main outputs (Fig. 1) obtained from the PLS technique are: (a) the variable importance in the projection (VIP) which indicates whether or not certain variables are important in explaining variation in the dependent variable; and (b) the standardised model coefficients which indicate the strength and direction of the effect. A positive and important (indicated by the VIP score) model coefficient indicates that the independent variable is correlated to a late occurrence of budburst. Where the model coefficient is negative and important, chill or heat values are correlated to early budburst. For (a), we adopted the standard procedure where VIP values greater than 0.8 are taken to indicate importance (Wold 1995). Further explanation and details of the PLS technique applied to phenological data sets are given by Luedeling et al. (2009a, b). All analyses were conducted using R software (R Development Core Team 2013), and the PLS analysis was implemented using the package 'chillR' (Luedeling 2013).

Effects of air temperature on the timing of budburst

The PLS regression procedure indicated that the timing of oak budburst was related to chill and heat accumulation during distinct periods of the year (see example in Fig. 1). After identifying the relevant periods for each provenance, we used a GLM to explore the relationship between the date of budburst and mean daily air temperature during both the chilling and warming periods. In order to help visualise and understand these combined effects of air temperature during the chill and heat accumulation periods on the timing of budburst, we used three-dimensional temperature response surfaces (see example in Fig. 4). These surfaces were constructed using the Kriging technique implemented in the R package 'fields' (Furrer et al. 2012).

Results

Variation between provenances and years

There were no *Q. robur* provenances originating from the southern range of latitudes (i.e. below 50.84°N. Table 1). When the analysis of the timing of budburst was restricted

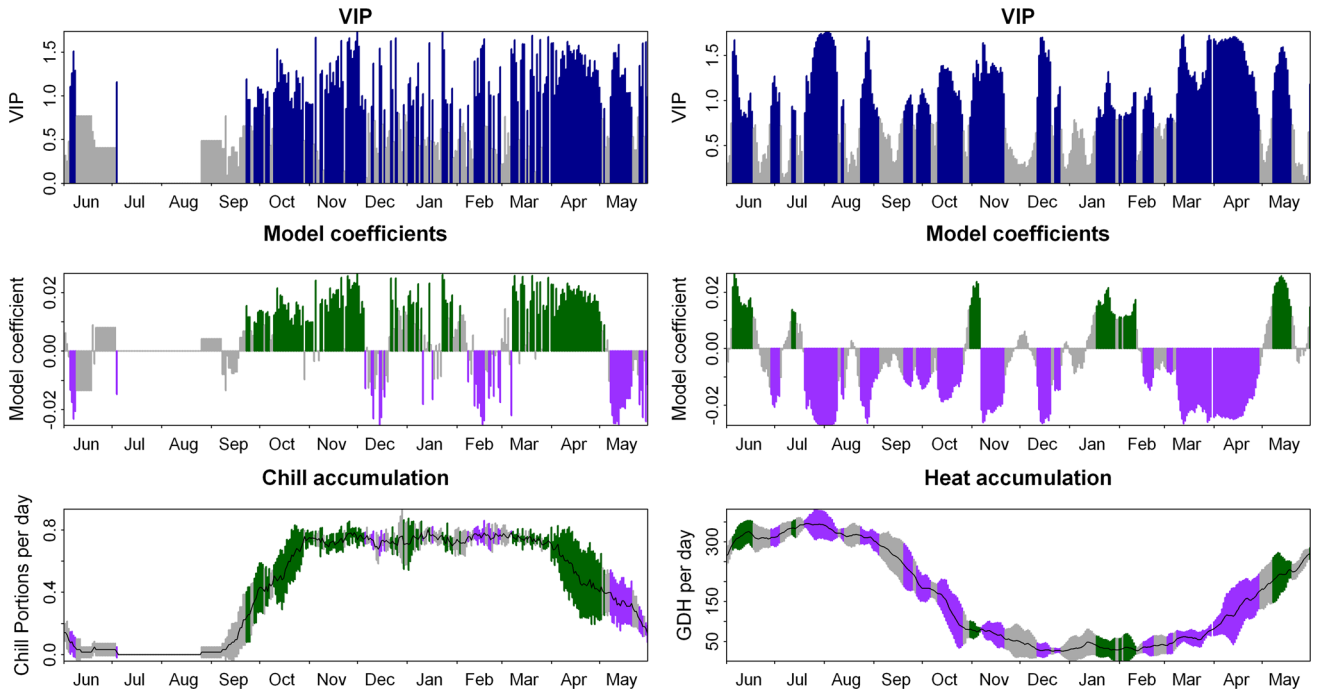


Fig. 1 Example of the results from the partial least squares (PLS) regression for provenance Gr at the Chiddingfold phenology trial, West Sussex. Variable importance in the projection (VIP, *top panels*), model coefficients (*middle panels*) and chill (Chill Portions) and heat (*GDH* Growing Degree Hours) accumulation rates (*bottom panels*). *Blue bars in the top panels* mean that VIP values are greater than 0.8, indicating that these variables are important for the model. In the *middle and bottom panels*, *purple colour* indicates that the model coefficients are important for the model and negative, whilst *green colours* indicate importance and positive model coefficients. The *black line in the bottom box* indicates the mean daily chill/heat accumulation rate, whilst the *grey*, *green* and *purple* areas indicate the standard deviation of the daily chill/heat accumulation rate over the 8 years of observations. (Color figure online)

to more northern latitude provenances only (50.84°N–53.13°N), there was no statistically significant difference in the date of budburst either between species (*Q. robur* vs *Q. petraea*, General ANOVA, $p = 0.071$), nor between species in different years (General ANOVA, $p = 0.08$). Therefore, the data from both species were treated as one group in all subsequent analysis.

The range of date of budburst averaged across all provenances between the 8 years of observations was 18 days, with 2007 being the earliest and 2013 being the latest (Fig. 2). The earliest and latest years also corresponded to the warmest and coolest mean late winter/early spring (February, March and April) air temperatures (8.8 °C in 2007 and 4.8 °C in 2013). Analysis of variance indicated that significant differences ($p < 0.001$) occurred in the timing of budburst between provenances within years and between provenances in different years. In 2007, buds of the earliest provenance (Be) started to burst around day 101, but in the late spring (2013) this did not occur until day 116. Budburst in all provenances was always complete by day 127, even in the late spring of 2013. Although the time period during which budburst occurred varied between 15 days (Be) and 22 days (Hh), Kendall's coefficient of concordance showed that there was no significant change (coefficient = 0.853; $p < 0.001$) in the order in which budburst occurred across provenances from the earliest (Gr and Be) through to the latest (Br and NL3).

Variation with latitude, altitude and continentality

The date of budburst was linearly related to latitude of origin with provenances from southern latitudes consistently leafing out earlier than those from more northerly latitudes, but there was significant variation across years. The relationship with the highest sensitivity (1.28 days later per degree north) occurred in 2006, whilst the lowest (0.44 days per degree north) was in 2013 (Fig. 3). Including altitude or continentality (either singularly or combined) did not significantly improve the fit of the GLM (data not shown).

Variation in the relevant periods influencing oak budburst

Relating the timing of oak budburst to chilling and heat accumulation using the PLS technique revealed distinct periods in the response of budburst (Fig. 1) and highlighted differences between the provenances. The relevant chilling period for each provenance was defined as the first day

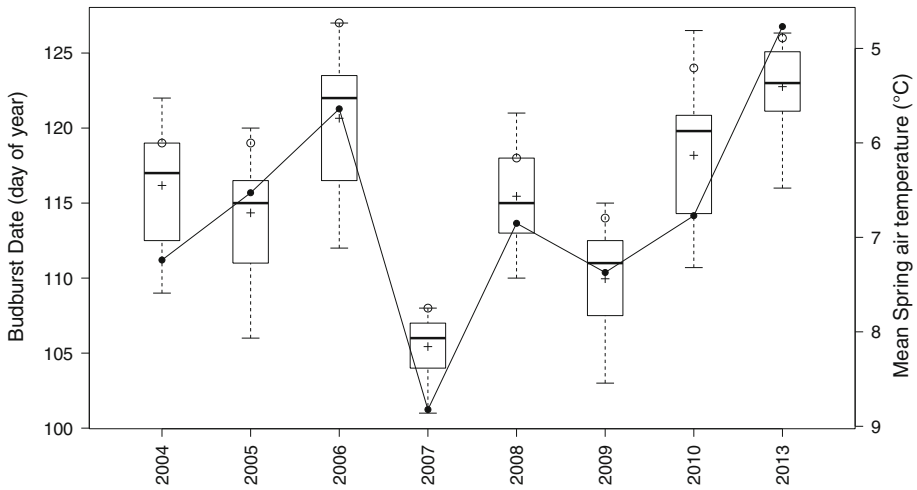


Fig. 2 Box–whisker graph of the annual median (*thick bar in box*), lower and upper quartiles (25 and 75 %; *top and bottom bars in box*) and the minimum and maximum (*whiskers*) day of year that budburst occurred at the Chiddingfold phenology trial, West Sussex. *Black crosses* are the mean date of all provenances. *Open circles* are the mean date for the local provenance (Wd). *Black line* with *filled circles* is the mean spring (February, March and April) air temperature at Alice Holt

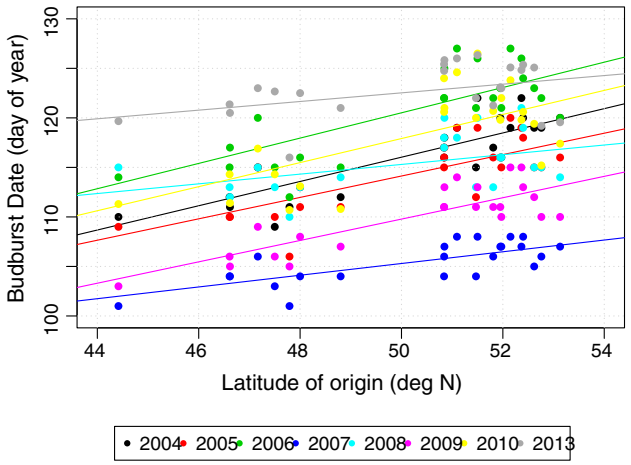


Fig. 3 Relationship of budburst date in each individual year with latitude of origin at the Chiddingfold phenology trial, West Sussex. *Solid coloured lines* are the best fit general linear models for each year. (Color figure online)

after the start of December when the model coefficients were negative and the VIP scores were >0.8 (indicating that chill accumulation led to earlier budburst), through to the last day in spring where these conditions were met. The critical periods for chill accumulation were not as consistently identified by the PLS model as the warming periods. For all provenances, there were times between the start of December and the onset of the critical warming period when the VIP scores were >0.8 and/or the model coefficients were positive (e.g. Fig. 1, for provenance Gr). This is likely to be related to periods when air temperature was below or close to freezing and therefore may not be effective for chill accumulation in oak trees. The relevant heat accumulation periods were more clearly defined. Generally, the most distinct and consistent periods occurred between mid-February and the start of May, when model coefficients for heat accumulation were mainly negative and VIP scores >0.8, indicating that heat accumulation during this period led to earlier budburst. A critical warming period was identified for each provenance: this was defined as the first point after the start of February when the model coefficients were negative and VIP scores were >0.8, through to the last day when these conditions were no longer met, which was actually the 5th of May for all provenances.

Response of oak budburst timing to temperature during relevant periods

Plant physiological understanding indicates that the timings of key phenological phases should be related to air temperature during both the chilling and warming phases and that these cannot be considered in isolation (Guo et al. 2015). In order to investigate this, a combined approach using a GLM and three-dimensional response surfaces was used. The GLM of budburst date and mean air temperature during the periods identified by the PLS analysis indicated a mean temperature-driven advance in budburst date during the warming period of 3.61 days/°C (standard error = 0.17 days/°C) and 0.99 days/°C (standard error = 0.16 days/°C) during the chilling period, both were highly significant ($p < 0.0001$). There was no significant interaction effect between air temperatures during the chill and warming periods on the date of budburst. The results for all provenances are shown in Table 2.

Plotting the date of budburst for each provenance as a function of air temperature during both the chilling and warming periods (see examples in Fig. 4) confirmed the results of the GLM analysis and demonstrated that budburst date contours were always relatively close to horizontal. These results demonstrate that spring temperature during the heat accumulation period was the dominant environmental driver of budburst date; mean daily air temperature

Table 2 Coefficients of a general linear model fitted to mean daily air temperature during the chilling and warming periods derived using the PLS analysis for 23 oak provenances at the Chiddingfold phenology trial, West Sussex

Provenance	Provenance term	Standard error (provenance term)	*p* value	Chill start (DOY)	Chill end (DOY)	Warming start (DOY)	Warming end (DOY)
De	4.30	1.26	<0.001	347	64	46	122
Co	3.28	1.26	<0.01	347	64	46	121
Ki	4.59	1.26	<0.001	347	63	46	120
We	5.46	1.26	<0.001	347	64	45	123
Pi	6.56	1.26	<0.001	347	64	46	121
Fa	7.44	1.26	<0.001	347	64	46	122
NL3	8.40	1.26	<0.001	347	64	46	121
Br[a]	9.03	1.31	<0.001	347	72	45	130
Bl	3.66	1.26	<0.01	347	64	45	124
Dy	5.42	1.26	<0.001	347	64	46	122
Sb	4.08	1.26	<0.01	347	64	45	121
Wd	8.18	1.26	<0.001	347	64	45	122
Vi	6.69	1.26	<0.001	347	63	46	121
Hh	5.31	1.26	<0.001	347	63	46	121
So	4.64	1.26	<0.001	347	63	46	121
No	−0.12	1.26	0.92	347	59	48	119
Or	0.61	1.26	0.63	347	63	46	120
Be	−3.14	1.26	<0.05	347	64	46	121
Ba	0.00	1.26	<0.05	347	59	49	119
Pr	3.23	1.26	<0.1	347	64	46	121
Ch1	0.44	1.26	0.73	347	63	47	120
Ch2	−0.67	1.26	0.59	347	63	47	119
Gr	−1.67	1.26	0.19	347	58	49	118

Budburst date = $142.27–0.99c_t–3.61w_t \pm$ provenance term

c_t mean air temperature during chilling period, w_t mean air temperature during warming period

[a] Provenance Br was not recorded in 2008 due to recorder error

during the winter chilling temperature had a much smaller, yet still significant effect.

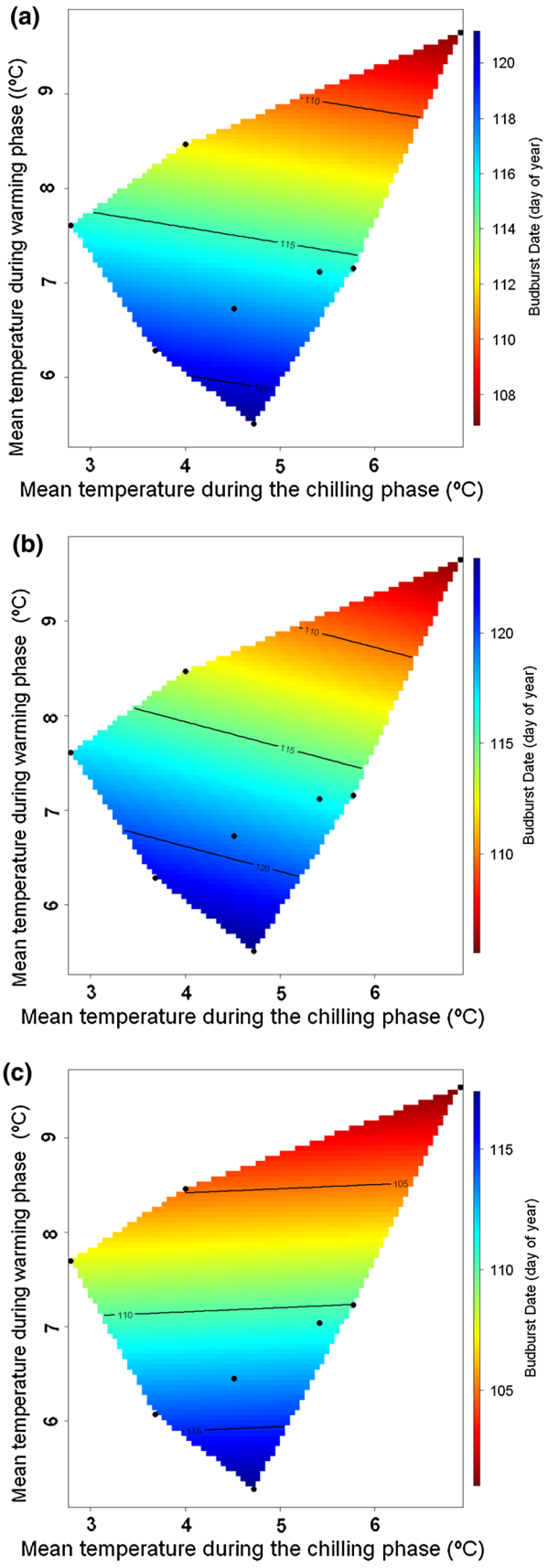
Date of budburst and exposure to cold temperature

Potentially damaging frost with a minimum air temperature of ≤−2 °C occurred near (within 10 days of) the mean date of budburst, i.e. between day 105 and day 125 at the Alice Holt Research Station in 31 out of the last 59 years. In order to assess the frequency that individual provenances were at risk from cold damage, we compared the date of budburst for each provenance with the latest minimum air temperature of ≤−2 °C. Provenances were assumed to be at risk when budburst had occurred (and therefore young developing leaves were exposed), prior to the last minimum air temperature of ≤−2 °C in each year (Table 3).

Developing leaves of the early flushing more southern provenances were exposed to potentially damaging cold air temperatures in three out of the 8 years that observations took place (2004, 2005 and 2008). Generally, the later flushing pattern of the more northerly provenances tended to 'protect' their young developing leaves, although there were a few instances when some individual trees of the more northerly provenances had reached budburst prior to the last ≤−2 °C minimum air temperature of the year (e.g. provenances Ki in 2008 and Co in 2005). The young developing leaves of the local provenance (Wd) were not exposed to potentially damaging cold air temperatures, even in years when provenances from similar latitudes (e.g. Bl in 2004 and Hh in 2005) were.

Discussion and conclusion

Variation in the timing of budburst by deciduous trees has important implications for the carbon balance of both individual plants and for the ecosystems to which they are



◀**Fig. 4** Date of budburst as a function of temperature during chilling and warming phases for provenances **a** De (northern range), **b** Dy (mid range) and **c** Gr (southern range) at the Chiddingfold phenology trial, West Sussex. The variation in *colour* reflects variation in the date of budburst, and the *black points* indicate actual budburst observations in each year. *Black lines* across each plot represent budburst date contours. (Color figure online)

integral (Keeling et al. 1996). Whilst early budburst may be seen as a strategy to maximise the potential time available for carbon uptake by extending the plant's effective growing season, it is not without risk. Depending upon the meteorological conditions in any given year, early budburst may expose new leaves to potentially damaging low air temperatures. Optimising budburst time is therefore a trade-off between maximising growing season length and minimising exposure to episodes of potentially damaging low air temperatures, which may result in a loss of photosynthetic area and reduced photosynthetic carbon gains (Leinonen and Hänninen 2002).

This study revealed important and statistically significant differences in budburst date between different provenances of *Q. robur* and *Q. petraea* over an 8-year period and confirms the earlier work of Kleinschmit (1993) and Deans and Harvey (1995) showing latitudinal variation in oak provenance phenology. The overall mean date of budburst across all provenances was day 113, very similar to a mean date of budburst (day 114) reported by Sparks and Carey (1995) from 167 years of oak phenology observations in eastern England, albeit from an unknown provenance. In our study, the range in mean budburst date between provenances varied from 13 to 22 days in different years, with a mean range of 18 days. This range is similar to the 20 days' range demonstrated in *Q. petraea* by Deans and Harvey (1995) in provenances with a similar latitudinal range to this study, but over a shorter observational period (3 years). The finding that there are differences in date of budburst when a range of provenances are grown at the same location and that this significantly correlated with latitude was not unexpected and is supported by a range of other studies. Deans and Harvey (1995) and Ducousso et al. (1996) both found that *Q. petraea* provenances from Austria and France showed earlier flushing than higher latitude German and British provenances. Liepe (1993) also demonstrated a significant positive correlation between latitude and budburst date. Reid (2011) monitored a range of provenances similar to those in this study at two more northerly trial sites in England, Wykeham in North Yorkshire (monitored in 2008 and 2009) and Arden in Warwickshire (monitored in 2008 only). When compared to the Chiddingfold site, the mean date of budburst across all provenances occurred 7 days later at the

Table 3 Per cent of individual trees exposed to air temperature ≤−2 °C following budburst for 23 oak provenances at the Chiddingfold phenology trial, West Sussex

Provenance	2004	2005	2006	2007	2008	2009	2010	2013
De	–	–	–	–	–	–	–	–
Co	–	8	–	–	–	–	–	–
Ki	–	–	–	–	8	–	–	–
We	–	–	–	–	–	–	–	–
Pi	–	–	–	–	–	–	–	–
Fa	–	–	–	–	–	–	–	–
NL3	–	–	–	–	–	–	–	–
Br	–	–	–	–	–	–	–	–
Bl	42	–	–	–	–	–	–	–
Dy	–	–	–	–	–	–	–	–
Sb	–	–	–	–	–	–	–	–
Wd	–	–	–	–	–	–	–	–
Vi	–	–	–	–	–	–	–	–
Hh	17	17	–	–	8	–	–	–
So	–	–	–	–	–	–	–	–
No	58	–	–	–	–	–	–	–
Or	42	33	–	–	17	–	–	–
Be	42	33	–	–	25	–	–	–
Ba	75	25	–	–	8	–	–	–
Pr	17	–	–	–	8	–	–	–
Ch1	25	–	–	–	–	–	–	–
Ch2	58	33	–	–	25	–	–	–
Gr	75	17	–	–	8	–	–	–

Arden site (1.21° further north than Chiddingfold) in 2008 and 13 days later at the Wykeham site (3.15° further north than Chiddingfold) in both 2008 and 2009. Reid (2011) also demonstrated a similar response to our current study, with budburst generally occurring earlier in more southern provenances, although these relationships were not statistically significant in 8 years or at either site in her study. Other experimental and observational investigations on oak in Europe have also not been as conclusive. Jensen and Hansen (2008) demonstrated a weak ($r^2 = 0.16$) but still statistically significant ($p < 0.036$) *positive* relationship between budburst date in different provenances of *Q. robur* and *Q. petraea* and source latitude, with the northern provenances slightly earlier than the more southern ones. However, that study used a much more northerly range of provenances (50.03°–60.45°N), it was an indoor nursery trial in an unheated glass house at an arboretum in Denmark (55°53′N, 12°31′E) and was observed over a single growing season.

An investigation into the biochemical and/or physiological mechanisms controlling budburst in oak is beyond the scope of this study. Our results do, however, confirm the large body of data showing that budburst in deciduous trees is under strong temperature control (Hänninen 1987, 1995; Cannell 1989) and that elevated spring temperatures result in earlier budburst (Polgar and Primack 2011). For all provenances, the variation in budburst date between years was mainly driven by differences in spring temperature. Differences in air temperature during the chilling period had smaller (lower sensitivity) yet still negative effect which we acknowledge is counter-intuitive. This may partly be because the range in mean winter temperatures during our observation period was only approx 4.6 °C and therefore 8 years of observations could be insufficient to enable the PLS technique to fully 'capture' the winter chilling requirements of the individual provenances. Indeed, Luedeling et al. (2013a, b) noted that at least 15-year worth of records are required for the PLS technique to produce reliable values for chilling and warming. However, our observations are consistent with other studies (e.g. Vitasse et al. 2009; Fu et al. 2013; Roberts et al. 2015) that have also demonstrated a low winter chilling requirement by oak trees.

The temperature sensitivity of spring budburst in temperate tree species has been analysed using both warming experiments (e.g. Vitasse et al. 2009; Morin et al. 2010; Fu et al. 2013) and long-term historical phenological observations (e.g. Sparks 2000; Menzel et al. 2006) with a wide range of results reported. For example, Dantec et al. (2014) reported a mean advance in budburst for *Q. petraea* along

an altitudinal gradient of 6.5 days/°C increase in spring temperature. Analysis of the 43-year record of budburst in *Q. robur* in southern England, extracted from Sparks (2000), showed an advance in budburst of 6.6 days/°C increase in spring temperature, whilst Vitasse et al. (2009) reported a similar response of 7.4 days/°C across several different French populations of *Q. petraea* from different altitudes. In experimental studies, the temperature sensitivity of *Q. robur* to spring temperature has been reported to lie between 2.4 and 6.3 days earlier per °C (Morin et al. 2010; Fu et al. 2013). In our study, the mean sensitivity was 3.61 days earlier per °C increase and was therefore within the range of values published in other studies. However, all these estimates are rather too low to account for the advance of budburst in temperate trees, which is estimated to be 2–3 days decade^{-1} on average during the last 50 years (Menzel et al. 2006; Richardson et al. 2006; Morin et al. 2010), i.e. 10–15 days total, over a period when mean spring temperatures have only risen by between 0.5 and 1.5 °C (e.g. for UK, Jenkins et al. 2008). There are a number of reasons for this mismatch between observed temperature sensitivity in short-term experimental or observational studies and the spring budburst phenological record. Firstly, the difficulty in deciding the appropriate spring warming period to use, so that for example, Dantec et al. (2014) calculated spring warming temperature over the period February 1–May 31 (which would exceed the period of budburst we observed here), whilst Sparks (2000) used January 1–March 31 (prior to all the observed budburst dates here). Selecting different periods over which to calculate the appropriate spring temperature will have a large effect on the estimated temperature response, but is problematic as the length of any required prior chilling period is not known. Secondly, the duration of a plant developmental phase is not linearly related to temperature, but its reciprocal, whilst the development rate is, above a threshold temperature and up to quite a high limit (e.g. Jones 1992). Therefore, the temperature sensitivity of duration assessed from relatively small inter-annual variations in temperature is an approximation and may well underestimate the rate change, particularly at warmer temperatures. This nonlinearity was evident in the study of three oak species by Morin et al. (2010). In addition, Morin et al. (2010) hypothesise that under strong warming conditions the temperature response of budburst may have become saturated and therefore the limiting factor in phenological advancement may have shifted from temperature to photoperiod requirements.

The southern provenances were repeatedly exposed to potentially damaging low air temperatures after budburst (although we acknowledge that we did not investigate whether these late incidents of cold air temperatures caused actual damage to the trees). Importantly, the southern provenances were exposed to potentially damaging low air temperatures even in the warmest spring of 2007.

Planting southern provenances of native tree species has been suggested as a climate change adaptation measure (e.g. Ray et al. 2010) as they should be better suited to future warmer growing conditions. The southern provenances planted at this south England site all broke bud earlier and would have had a slightly earlier start to their growing season (Fig. 2). In this study, the date of budburst in all provenances was mainly determined by spring air temperature, with a much lower sensitivity to air temperature during the winter chill accumulation phase. This would suggest that under current climate conditions their chilling requirements are largely fully met. However, because of our inability to measure it in situ, there is uncertainty about their actual chilling requirement, which still requires further investigation. A number of recent studies (e.g. Baldocchi and Wong 2008; Luedeling 2012) have demonstrated that winter chill has been declining in some temperate and subtropical regions areas and that this trend is likely to continue declining in the future, although to what extent this will affect oak trees in temperate regions is still uncertain.

In summary, we have demonstrated differences in the response of budburst to spring temperature across a range of European oak provenances grown at a single site. Budburst in provenances from more southern locations consistently occurred earlier than those from more northerly latitudes. For all provenances, the timing of spring budburst was strongly related to air temperatures during the spring warming period, and under current climatic conditions the chilling requirement of all provenances appeared to have been easily met.

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Chapter 5 - Can upward-facing digital camera images be used for remote monitoring of forest phenology?

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Can upward-facing digital camera images be used for remote monitoring of forest phenology?

Matthew Wilkinson*, Edward L. Eaton and James I.L. Morison

Centre for Sustainable Forestry & Climate Change, Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK

*Corresponding author: Tel: +44(0)300 067 5758; Fax: +44(0)420 520180; E-mail: matthew.wilkinson@forestry.gsi.gov.uk

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Digital hemispherical photography is a valuable method for monitoring changes in the biosphere's response to climate change. In forests, cameras have often been fitted to existing towers and masts. However, such towers are logistically difficult and expensive to install. Ground-based automatic camera systems offer an alternative that removes the barriers associated with above-canopy photography, but to date there have been few comparisons between upward- and downward-facing images at the same site. This study addresses this issue, by comparing a pair of cameras, one ground-based, one tower-based, viewing the same trees in a deciduous oak (*Quercus robur* L.) plantation forest in south-eastern England. Over 6 years, the upward-facing ground-based camera system was able to detect key spring phenological events to the same extent as the more usual downward-facing camera (mean difference of 2 days for green-up date). However, the upward- and downward-facing systems were less well-matched in detecting specific events at the end of the growing season, although both systems displayed similar temporal trends. Upward-facing cameras can therefore act as a reliable and comparable alternative to tower-based phenocam systems, as well as being more suitable for wider spatial coverage without the need for expensive installation infrastructure. In addition to the increased ease of access with upward-facing camera systems, the images from them also allow canopy structural dynamics such as canopy closure to be estimated.

Introduction

Some of the most visibly obvious outcomes of recent climate change are shifts in phenology, the timing of the seasonal activity of plants and animals. Numerous different approaches (e.g. manual observations, manipulation experiments and satellite remote sensing) have been used to monitor, document and understand the phenological changes that have been observed across a range of different ecosystems. In addition to being an important indicator of climate change, the implications of altered phenology are numerous. In plants, such implications range from changes in plant productivity and carbon budgets (Ciais *et al.*, 2013), to disrupted synchrony between plant hosts and their insect pollinators (e.g. Schenk *et al.*, 2017) and increased risk of exposure to damaging frosts (Vitasse *et al.*, 2014).

Traditionally, phenological measurements have been recorded by observers, a system which is subjective, labour-intensive and generally lacks temporal resolution. Therefore, the use of repeat digital photography for phenological monitoring of natural and managed ecosystems is an attractive alternative that has proliferated in recent years. This 'near-surface remote sensing' approach also enables images to be analysed in a quantative manner. Two vegetation indices have been widely used to detect foliage phenology: the relative brightness of the green channel (e.g. Ahrends *et al.*, 2008; Richardson *et al.*, 2009) and the Green Excess Index (Woebbecke *et al.*, 1995). In this study we use the former approach. Standardized systems, operational protocols and data collection networks such as the European Phenology Camera Network (http://european-webcam-network.net/) have been developed in an attempt to harmonize image and data collection. In forests, these 'phenocam' systems have generally been deployed on existing research infrastructures such as tall towers or masts to provide appropriate views of forest canopies, especially for the ground-truthing of remotely sensed data. However, such towers, masts and canopy cranes are both logistically difficult to install and are expensive. By removing the need for installation above the top of the canopy, ground-based camera systems (pointing upwards) could provide an attractive alternative with numerous logistical, cost and safety benefits. The purpose of this study was therefore to investigate the suitability of ground-based digital cameras for the remote monitoring of forest phenology. This was achieved by comparing the red–green–blue signals from an upward-facing camera system with an identical system mounted above an oak (*Quercus robur* L.) forest canopy, facing downwards. Key phenological events were identified for both camera systems to determine if there were any differences in the timing of detection of green-up, maturity, senescence or dormancy.

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Methods

Study site

The study site was located in the Straits Inclosure, Alice Holt Forest (51°07′ N, 0°51′ W), in south-eastern England. The site, which is an 80-year old deciduous oak plantation, has been the focus of much scientific research over the past 20 years including carbon and greenhouse gas balance research (e.g. Heinemeyer *et al.*, 2012; Wilkinson *et al.*, 2012; Pinnington *et al.*, 2016; Wilkinson *et al.*, 2016; Pinnington *et al.*, 2017; Yamulki and Morison, 2017) and long-term ecological research (e.g. Pitman *et al.*, 2010; Benham *et al.*, 2012). The forest is a relatively flat area with an average elevation of 80 masl and the surrounding landscape consists of mixed lowland woodland and both arable and pasture agricultural land. The main tree species is oak, but other species, including European ash (*Fraxinus excelsior* L.), *Q. petraea* (Mattuschka) Liebl. and *Q. cerris* L., are also present. Mean canopy height is 20 m and the long-term mean peak leaf area index (LAI) calculated from cumulative LAI measured using litterfall traps is 5.92 m^2 m^{-2}. The climate of the region is mild, temperate and oceanic, with a long-term mean (1971–2000) screen annual air temperature of 9.6°C and a mean annual precipitation of 779 mm; a full site description is given in Wilkinson *et al.* (2012).

Camera systems

This study was designed to compare the phenologically relevant information extracted from images taken by an upward-facing ground-based camera with those from a downward-facing (above-canopy) camera over 6 years (2011–2016). An upward-facing digital camera (Coolpix 4500; Nikon, Japan), fitted with a circular hemispherical lens (FC-E8 fisheye lens; Nikon, Japan, field of view 180°) was fixed to the roof of an instrumentation cabin at a height above ground level of 3.0 m, 6.0 m north-west of the 26 m tower. Importantly, this camera was located above the ground vegetation and shrub layer. The camera and associated electronics were housed in a weatherproof box, with a transparent plastic dome fitted over the upper side to ensure an unobstructed view of the underside of the forest canopy. An identical camera system was mounted on the tower at a height above ground level of 22.0 m. The weatherproof box was fixed to a pole extending 2.5 m away from the south-west side of the tower; the box was inverted to give an uninterrupted view to the horizon over the top of the forest canopy. Details of this camera system are described in Mizunuma *et al.* (2013). Some of the same oak and ash trees were visible in images from both camera systems. A series of example images from the two camera systems taken on the same days in 2012 is given in Figure 1. The images were collected as part of the Phenological Eyes Network (http://pen.agbi.tsukuba.ac.jp/index_e.html), with which this site is associated. Both camera systems were connected to computers located in the instrumentation cabin via power over Ethernet cables. Images from both camera systems were taken every half hour from 04.20 to 21.50 GMT throughout the 6-year period using the open software PHOTOPC (http://www.lightner.net/lightner/bruce/photopc/) to control and automate the process. The white balance setting was fixed for both cameras. The images were stored as compressed JPEG format (resolution 2272 × 1704 pixels, with three channels of 8-bit Red–Green–Blue (RGB) colour information) and were downloaded weekly for subsequent analysis.

Image selection and colour balance analysis

Due to their opposite viewing angles, different selection criteria were required for the upward- and downward-facing images. For the downward-facing system, it was necessary to minimize variation in the lighting conditions produced by changes in solar angle over the course of a day: only images taken at 11.30, 12.00, 12.30 and 13.00 GMT were considered for analysis. Variations in lighting conditions were less problematic for the upward-facing system, as the trees intercepted a large proportion of the direct sunlight. However, rain and especially condensation on the protective domes significantly reduced the capture of useable images from the upward-facing system, therefore images over a longer time period (07.50, 09.50, 12.20 and 16.50 GMT) were considered for analysis. Each of these images (upward- and downward-facing) were checked by the same trained individual and rejected when frost, snow, condensation or rain droplets appeared in any part of the image. From this subset (Table 1), one image per day was selected for subsequent analysis. The longest gap between images was 119 days which occurred during the winter leafless period between 7 November 2014 and 6 March 2015, although this was due to instrument failure rather than the image selection procedure. The longest gap between images resulting from the selection procedure was 17 days, which occurred between 17 June and 4 July 2015.

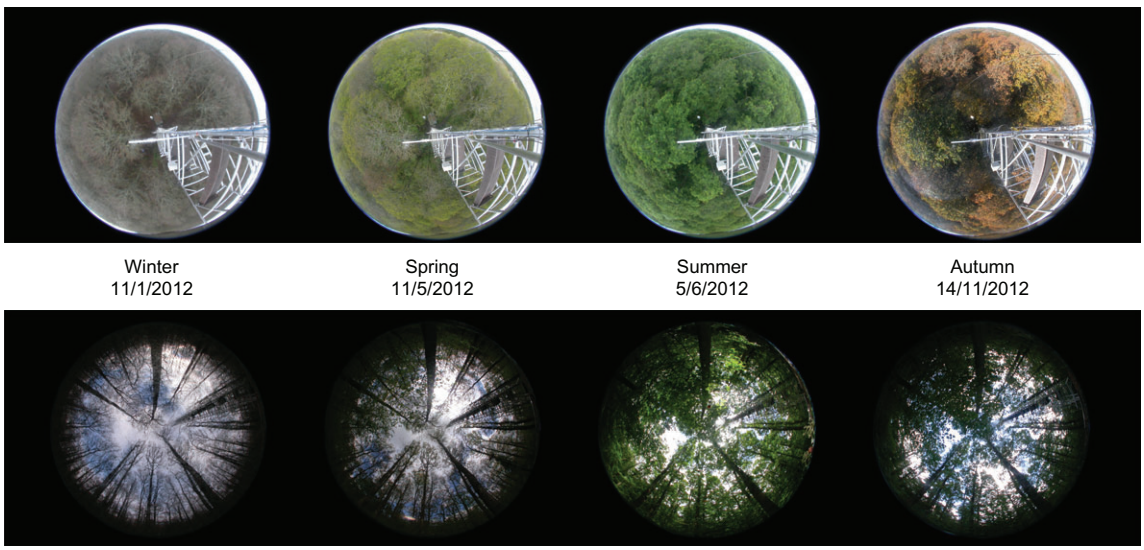

Figure 1 Example original images taken from the downward-facing (top panel) and upward-facing (bottom panel) camera systems on the dates shown, at the Straits Inclosure, Alice Holt Forest, Hampshire, UK.

Table 1 Total number of images taken between 04.20 and 21.50 GMT (upward- and downward-facing camera systems) and the total number of images used for DN_{RGB} analysis between 2011 and 2016 at the Straits Inclosure, Alice Holt Forest, Hampshire, UK

Year	Upward-facing		Downward-facing	
	Total	Analysed	Total	Analysed
2011	13 140 (100)	318	12 045 (100)	324
2012	13 076 (99.2)	285	11 975 (99.1)	299
2013	12 511 (95.2)	218	12 015 (99.8)	309
2014	11 611 (88.4)	279	10 520 (87.3)	278
2015	10 904 (83.0)	228	11 455 (95.1)	248
2016	12 230 (92.8)	228	10 072 (83.4)	196

Figures in brackets are per cent data capture.

The RGB digital number is a unitless numerical value for each pixel in a digital image proportional to the intensity of the red, green and blue colour channels (e.g. Richardson *et al.*, 2007; Sonnentag *et al.*, 2012). For both the upward- and downward-facing images, the area in each image containing the tower was excluded from the target area (Figure 2). The strength of each colour signal (S_R, S_G and S_B) relative to the total of RGB (Gillespie *et al.*, 1987) was calculated for the target areas using the following equations:

$$S_R = \left[\frac{DN_R}{DN_R + DN_G + DN_B}\right] \times 100 \quad (1)$$

$$S_G = \left[\frac{DN_G}{DN_R + DN_G + DN_B}\right] \times 100 \quad (2)$$

$$S_B = \left[\frac{DN_B}{DN_R + DN_G + DN_B}\right] \times 100 \quad (3)$$

where DN is the digital number of each respective colour channel. The analysis was performed using R software (R Core Team, 2017) and the image colour analysis was implemented using the package 'Phenopix' (Filippa *et al.*, 2016).

Statistically significant breakpoints in the time series of S_G, coinciding with the important phenological events of green-up, maturity, senescence and start of dormancy were identified. Each year was split into an appropriate time window, based on Day of Year (DOY) (green-up DOY 80–150, maturity DOY 125–180, senescence DOY 250–335 and dormancy DOY 290–365) and a piecewise linear regression model was fitted to each subset of data, using the R package 'SiZer' (Sonderegger, 2012). Each year was analysed separately. Where the S_G time course data were missing, it was not possible to derive a breakpoint value for that period. Differences between the two systems for each set of breakpoint dates were tested for significance using a paired *t*-test (R Core Team, 2017).

Canopy gap fraction and canopy closure analysis

In addition to the phenological information that can be extracted from the upward-facing hemispherical photographs, there is also inherent information about the structure of the forest canopy. One of the benefits of the repeated upward-facing images with a sky background is that the structural dynamics of forest canopy development can be measured, which is not possible for the downward-facing images with a dark ground background. The seasonal pattern of canopy closure was extracted from the target area of a subset of images for each year,

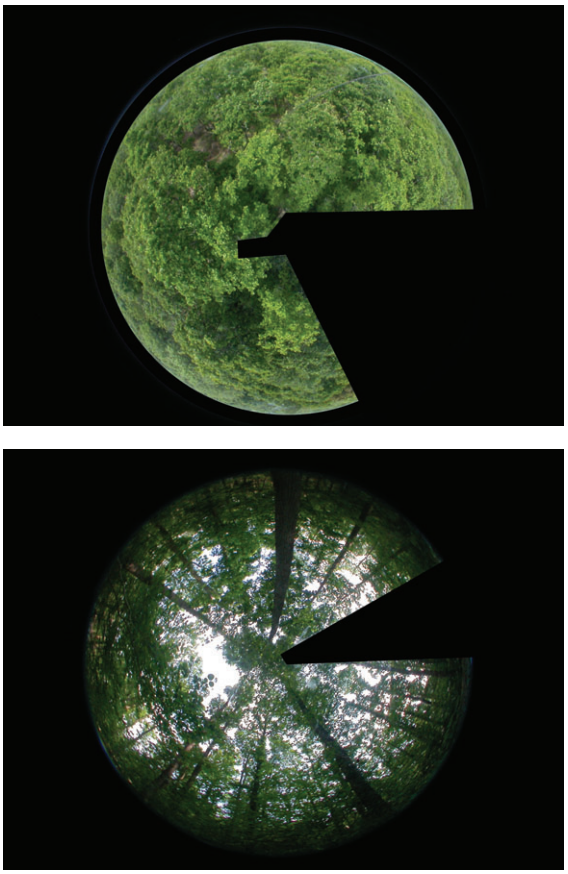

Figure 2 Example upward- and downward-facing images showing target areas for Digital Number DN_{RGB} measurements, with tower area and perimeters excluded, and rotated so that top of image is in the direction of north.

using the LAI-CAM programme within CIMES-FISHEYE (Gonsamo *et al.*, 2011). CIMES-FISHEYE is a package of free programmes for the analysis of hemispherical photographs of the undersides of forest canopies and can be used to extract key canopy attributes. For these images, an additional quality control procedure was required: in order to minimize the effects of wind, and therefore movement of the upper canopy, images were rejected when the average wind speed measured using a sonic anemometer (model Solent R3, Gill Instruments, Lymington, UK) ~6 m above the canopy for that corresponding period was >1.5 ms^{-1}. From this subset, one image per day was selected for subsequent analysis. These images were rotated by 153° clockwise to orientate north to the 'top'. The images were then split in to the red, green and blue channels, and the blue channel selected in order to give the best contrast between sky (background) and forest canopy cover (foreground). Each pixel within the image was subsequently classified as either background or foreground using a threshold value of 120. Different automatic methods to determine the threshold value were examined: the IsoData approach (Ridler and Calvard 1978) and the Minimium algorithm (Prewitt and Mendelsohn 1966). Neither of the automatic methods were as sensitive as a manual threshold of 120. All image preparation was done using the free image processing software ImageJ (https://imagej.nih.gov/ij/download.html). Canopy gap fraction was extracted for each individual quality controlled image using GFA, the core programme of the CIMES-FISHEYE package. The results from GFA were subsequently passed to the LAI-CAM sub-programme which was used to calculate canopy closure (CC), the reciprocal of canopy openness (CO), defined as the area

fraction of the sky hemisphere (180°) that is unobstructed by canopy elements when viewed from a single point. A full description of the method is given in (http://jmnw.free.fr/). To compare these structural data with satellite-based observations, the MODIS Collection 5 Land Products was obtained (ORNL DAAC, 2017) for 2011–16 inclusive (FPAR, MOD15A2, 8-day composite 1 km resolution) for a 1 km × 1 km grid centred on the Straits flux tower. FPAR is the fraction of photosynthetically active radiation (400–700 nm) absorbed by green vegetation.

Results

Upward- and downward-facing camera colour signals

A similar seasonal pattern of S_G, characteristic of deciduous broadleaved forests, was derived from the images taken by both camera systems in all years (Figure 3a–f). Following a low over-winter period when the canopy was leafless, S_G rapidly increased after the onset of the growing season due to bud burst and leaf development. Following a spring peak in S_G, the signal declined and then stabilized, more so in the downward-facing images than the upward-facing (DOY 180–300). There was a closer agreement in the absolute summer values in some years (e.g. 2015) than others (e.g. 2012 and 2013). The end of the growing season was also clearly identifiable and well synchronized in both systems, and was characterized as a rapid reduction in S_G, which corresponded to the onset and subsequent progress of autumn senescence (DOY 275–330). Because of the poorer image quality in the autumn, there were insufficient data to compare the estimated dates of start of dormancy from the two systems. Overall, S_G extracted from the two systems was well synchronized although there was generally more day-to-day scatter in S_G from the upward-facing system.

In contrast to S_G, there was a small decrease in S_R in both the systems as the canopy developed during spring. S_R remained low over the summer period (DOY 150–300) and then increased rapidly from DOY 300 before dropping back down to a relatively stable over-winter level. The seasonal pattern of S_B was generally the inverse of S_G. Following a relatively stable

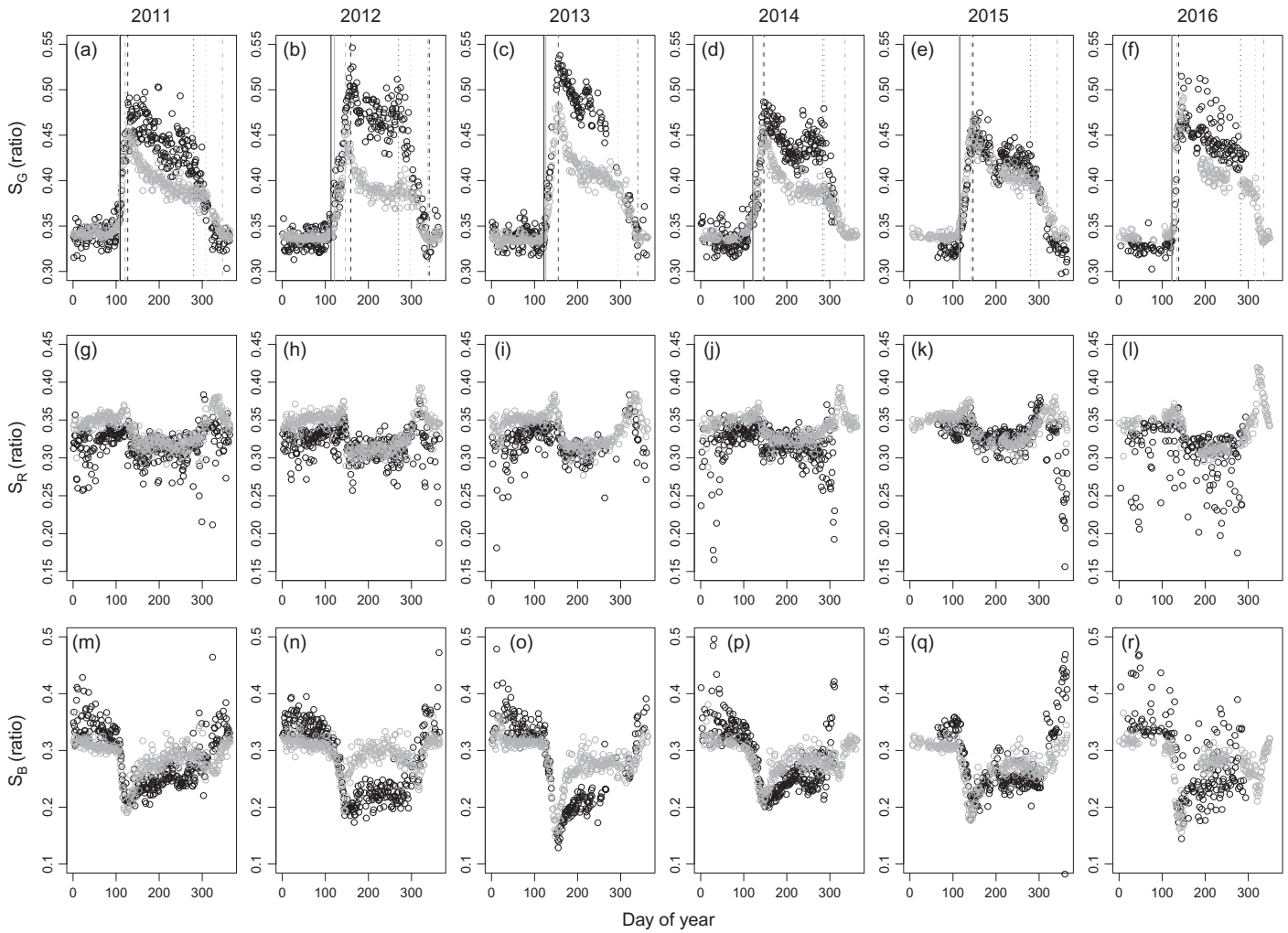

Figure 3 Seasonal pattern of colour strength in green, S_G (top row, a–f: 2011–16), red, S_R (middle row, g–l: 2011–16) and blue S_B (bottom row, m–r: 2011–2016) in daily images taken by an upward-facing (black open circles) and a downward-facing (grey open circles) camera systems at the Straits Inclosure, Alice Holt Forest, Hampshire, UK. Vertical lines are key phenological events identified by breakpoint analysis (solid line = green-up, dashed line = maturity, dotted line = senescence, dot-dash line = start of dormancy, colours as for the circles).

over-winter level, S_B dropped rapidly at the same time as S_G increased. S_B reached a seasonal minimum in spring, before increasing again over summer, although this increase was more pronounced in images from the downward-facing than the upward-facing camera system (for example see Figure 3n,o). In both systems, S_B increased from around DOY 300 onwards and then stabilized over winter, though with more scatter in the signal from the downward-facing camera system.

Identification of key phenological phases

The significant breakpoints in the time course of S_G, associated with key phenological transitional points in the annual cycle of a deciduous oak forest are shown in Figure 3a–f (see vertical lines) and Table 2. In all years and in both systems the onset of spring green-up identified by the breakpoint analysis occurred between DOY 108 and 126. There was a close agreement in the mean values for green-up over the 6 years (DOY 119 and DOY 117 for the downward- and upward-facing cameras respectively) and no statistical difference ($t(5) = -1.210$, $P = 0.280$) between the two sets of observations. The maximum difference detected was 8 days (2012) but in all other years the difference was always less than 5 days. In contrast, there was a statistically significant difference in the estimated dates for maturity ($t(5) = 3.4109$, $P = 0.019$) and senescence ($t(5) = -3.101$, $P = 0.053$) by the two systems. The estimated dates of maturity were always later from the upward-facing system with a mean difference of 5.1 days and a maximum difference of 12.3 days (2012). In contrast, the estimated dates of senescence were consistently earlier from the upward-facing system compared with the downward-facing camera.

Canopy structural dynamics

The time series of canopy closure derived from the upward-facing images was consistent with the canopy dynamics of a deciduous oak forest in south-eastern England. Spring development was earliest in 2011 coinciding with warm spring conditions (mean spring temperature = 10.4°C). Once fully developed, canopy closure remained high throughout the summer and autumn. The timing of the increase in canopy closure (Figure 4) generally coincided well with the increase in spring S_G (Figure 3) detected from this camera (DOY 100–150). At the end of the growing season the decline in S_G and decline in canopy closure were not synchronous. Canopy closure remained high for longer than S_G, and only started to decline once the leaves began to fall, after around DOY 310 (Figure 4). The delay between the onset of senescence and the decline in canopy closure varied considerably between years ranging from 15 days (2014) to 38 days (2012). Canopy closure derived from the hemispherical photos showed closely similar seasonal patterns to the FPAR values derived from MODIS satellite images for the forest in all years. These two independent datasets are not readily compared, because they were not always synchronous and are for a single point within the forest compared with a 1 km × 1 km grid square covering the forest. However, the strong similarity in seasonal patterns provides a useful verification of this method.

Table 2 Day of year of statistically significant breakpoints in the time course of S_G associated with green-up (GU), maturity (M), senescence (S) and dormancy (D) and the difference (Δ, days) between the two for an upward-facing (Uf) and downward-facing (Df) camera system at the Straits Inclosure, Alice Holt Forest, Hampshire, UK

Year	GU			M			S			D		
	Uf	Df	Δ	Uf	Df	Δ	Uf	Df	Δ	Uf	Df	Δ
2011	110	108	2	127	121	6	280	308	**−28**	324	347	**−23**
2012	113	121	−8	159	147	**12**	270	297	**−27**	341	338	3
2013	122	126	−4	156	154	2	Na	294	Na	340	340	0
2014	121	123	−2	147	145	2	284	288	−4	Na	335	Na
2015	115	114	1	147	142	5	280	293	**−13**	Na	342	Na
2016	122	122	0	138	134	4	Na	317	Na	Na	335	Na

Bold type indicates a difference >10 days.
Na indicates that S_G data was missing for that period and therefore it was not possible to derive a breakpoint value.

Discussion

Over the 6 years of this study, the time course of colour signals extracted from the upward- and downward-facing camera systems were well synchronized and both described a similar seasonal pattern of the deciduous oak canopy. The timings of both spring green-up and maturity derived from the green index extracted from the two camera systems were similar. However, estimated dates of autumn senescence and start of dormancy derived from the extracted colour signals did not compare as well. This was due to a combination of missing observations and a high level of scatter in the S_G values from the upward-facing camera system at that time of year. We also acknowledge that the main constraint of this study is that it was based on a comparison of only one pair of cameras. Therefore, some of the observed differences in dates may be a result of the specific locations and canopy views, rather than the differences in upward vs downward systems *per se*. However, the 6-year duration of data analyses has ensured that we were able to compare the systems over a wide range of meteorological conditions.

There has been an increase in the number of studies published over the past 10 years using plant phenological data inferred from various different camera systems (e.g. Sonnentag *et al.*, 2012, Wingate *et al.*, 2015; Moore *et al.*, 2017) which have reported important information about the biosphere's response to environmental and climate change. The majority of these published studies, especially from instrumented forest sites, have camera systems installed on towers to complement other above-canopy environmental measurements. However, such infrastructure is expensive to install and maintain; requires specialist skills to access, making instrument failure more difficult to repair; and the quality of the recorded images is highly dependent on solar angle and weather conditions. One possible solution to many of these problems is to use ground-based cameras. We acknowledge that there may be some disadvantages to ground-based systems. For example, they may be subject to higher levels of data loss due to rain or snow, although this could be avoided by automatic cleaning systems. In addition, in dense forests canopies very low levels of light may

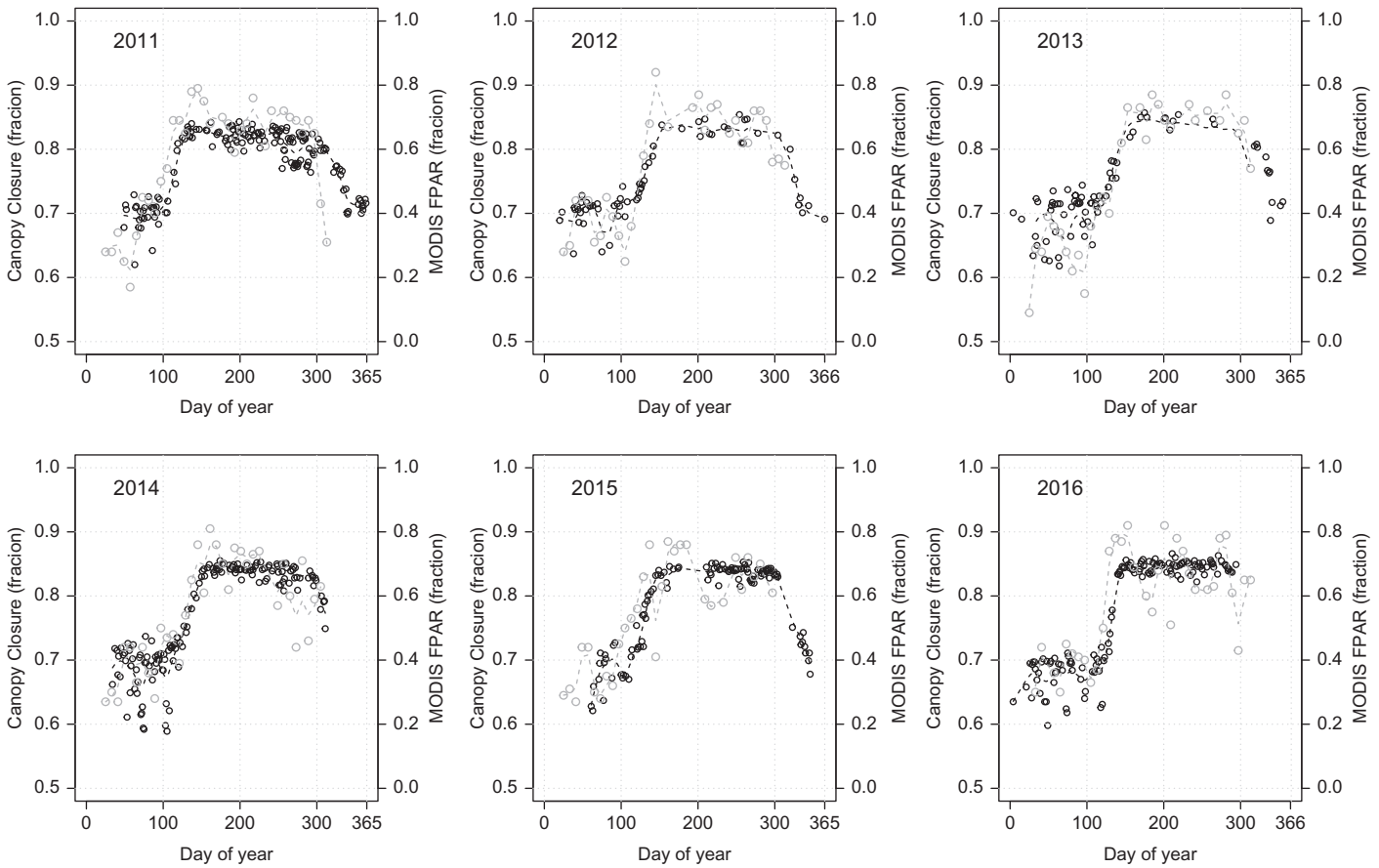

Figure 4 Seasonal pattern of canopy closure (black open circles) computed from daily upward-facing hemispherical images and MODIS fraction of intercepted photosynthetically active radiation (FPAR, grey open circles) for a 1 km × 1 km grid centred on the flux tower for 2011–16, at the Straits Inclosure, Alice Holt Forest, Hampshire, UK.

make this approach unsuitable although newer digital cameras have much higher light sensitivity. Yet where site conditions permit, ground-based camera systems are far more akin to traditional manual phenological observations, where the observer was stood on the ground looking upwards at the underside of the canopy.

One of the few studies similar to ours, albeit over a shorter time period, was that of Nagai *et al.* (2013). This study also compared the DN_{RGB} values from upward- and downward-facing images (over three years) from a deciduous broadleaved and an evergreen coniferous forest in Japan. Consistent with our findings, Nagai *et al.* (2013) demonstrated that upward-facing camera systems were able to detect canopy-level phenology in a deciduous broadleaved forest almost as well as from downward-facing images. However, at an evergreen coniferous forest they found that the upward images did not capture the canopy level phenology, which the authors attributed to the light attenuation characteristics of this conifer stand. Moore *et al.* (2017) also utilized images from upward- and downward-facing phenocams at an Australian tropical savannah site, although their study did not explicitly compare the performance of the differing camera systems.

Whilst overall there was a close agreement in the timing of the colour signals from the two different but matched camera systems, even in the winter leafless periods the colour signals differed between the two, with stronger blue and less red components in the upward facing images (Figure 3). As the canopy developed during the summer the S_G values computed from the upward-facing images (Figure 3) were usually substantially higher than the corresponding values from the downward-facing system, which is linked to the much larger decrease in S_B in the upward-facing images. We suggest these different seasonal patterns occur in part because of the changes in light absorption by leaf pigments, but also because of the differing illumination conditions and views of the camera systems. The upward facing images have a large proportion of skylight (higher blue content) in the winter, which reduces as the canopy expands, while the downward facing images have a background largely of dark soil and litter (producing a higher red content), which reduces as the canopy expands and starts to reflect some skylight, as well as green. At the end of the growing season, the piecewise linear regression did not identify the onset of senescence in S_G from the upward-facing images as clearly as that in S_G from the downward-facing ones. This was in part due to missing data, where images had been rejected due to rain, fog or fallen leaves reducing the quality of the upward-facing images.

In addition to the phenological information derived from the analysis of colour signals, we have demonstrated that

upward-facing camera systems can usefully provide further information about the structural dynamics of a broadleaf forest. The degree of canopy closure is a key parameter for many forest biophysical process, such as light interception, water and energy balances (Law *et al.*, 2001), and has implications for the composition of forest floor vegetation. If this information can be collected via the same method as phenological data, this provides a powerful and efficient tool for forest monitoring. In addition, the greater ease and lower cost with which ground-based systems can be deployed could allow data collection over a wide area with multiple cameras which offers a clear advantage in heterogeneous forest light environments. Indeed, Bianchi *et al.* (2017) have recently shown how canopy structural characteristics can be estimated using very inexpensive smartphone cameras with hemispherical lenses, devices that might lend themselves to multiple installations. A combined approach which builds on the long history of hemispherical photography to derive forest structural parameters (e.g. Evans and Coombe, 1959) provides a semi-automated method which could easily be applied to other monitoring sites and which has numerous advantages over traditional manual systems. Manual hemispherical photography is not only time consuming, but the most suitable lighting conditions are generally close to dawn or dusk, which limits data collection. Furthermore, a reliance on manual methods can result in coarse re-visit frequency, which may miss key phenological, physiological or disturbance events. Automated upward-facing camera systems, when combined with rigorous quality control procedures, can therefore overcome some of these problems. Several previous studies have demonstrated the utility of upward-facing camera systems for monitoring structural parameters. For example, Ryu *et al.* (2012) used a number of upward-facing cameras to describe on a daily time step the dynamics of LAI for an oak savannah ecosystem in California. The combination of these two different sources of information on light transmission and colour signals may provide a valuable source of data and therefore model parameters, that would not be available from a site equipped solely with a downward-facing camera system.

Conclusion

This study has clearly shown that the images from upward-facing camera systems can be used to quantify deciduous forest *spring* phenological events equally as well as those from the more usual downward-facing systems. The timing of spring budburst is frequently used as an indicator of climate change and was detectable in the upward-facing images, although detecting the start of autumn senescence was more problematic. Upward-facing images can also be used successfully to measure forest structural canopy dynamics. As ground-based upward-facing camera systems do not require the extensive infrastructure of tower-based downward-facing systems and the problems inherent with their installation, maintenance and use, they are much more suitable for widespread deployment, for forest monitoring and to improve our understanding of the effects of climate change.

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Conflict of interest statement

None declared.

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Chapter 6 – Background literature and scientific contribution

6.1 Aims and objectives

The aim of this chapter is to provide an assessment of the contribution that each of my four first authored peer reviewed publications has made to the overall body of scientific knowledge and understanding relating to temperate forests functioning in a changing climate. The objectives are, firstly, to provide the background context and basis for each publication and, secondly, to appraise how each publication related to the existing knowledge and research methods at the time of publication. Further objectives are to highlight key findings from each publication, demonstrate the contribution that each publication has made to subsequent scientific studies, meta-analyses and methodologies and, where relevant, to highlight aspects of science out-reach or wider communications that have developed because of this work. The chapter is organised by year of publication.

6.2 Peer reviewed journal papers – scientific contribution

Over the past 20-25 years, continuous, direct measurements of CO_2, H_2O and energy fluxes using EC have become a powerful tool in improving the understanding of gas and energy exchange between forests and the atmosphere (Baldocchi et al., 2002). Concurrent with technological and instrumentational developments that have improved the quality and ease of data collection, collaborative regional and international networks (e.g. Euroflux, FLUXNET) have linked individual EC sites. This collective effort by researchers from around the world now provides a valuable resource enabling the scientific community to investigate fundamental question related to the biophysical factors influencing ecosystem functioning.

Wilkinson et al. (2012) reported the results from 12 years (1999-2010) of near continuous CO_2 flux measurements using EC at an 80-year-old oak woodland in south-eastern England. This EC site was originally established in March 1998, the author took over responsibility in September 2001 and has managed it ever since. Prior to the publication of this paper only limited summary data from the site had previously been published (e.g. Read et al., 2009). This paper was therefore the first time that the annual sums of CO_2 net ecosystem exchange (NEE) and its component assimilatory (gross primary productivity, GPP) and respiratory (ecosystem respiration, R_{eco}) fluxes from this long-term study site had been published in detail. This paper also quantified the magnitude and examined the causes of the inter-annual variability observed in the partitioned fluxes, and assessed their relationship with key climatic and biotic drivers. The paper highlighted that the inter annual variation in NEE was large (SD = 115 g C m^{-2} y^{-1}), in part because it is the difference between two much larger fluxes of GPP and R_{eco}. Other key findings from this long-term work included, the demonstration of a strong correlation (r^2 = 0.7, $p<0.001$) between leaf area index (LAI) and GPP and resilience to the

2003 Europe wide heatwave. In the paper, we hypothesised that the latter of these was most likely due to good water supply from the heavy clay soils at this site.

Despite there being several active forest EC flux sites across Europe at the time of publication, very few had been running as long as the Alice Holt site. Other sites that had a comparable length of observations were generally from evergreen coniferous forests and therefore were not characteristic of deciduous forests in the south of England. Prior to the publication of this study, only one other long-term study from a UK forest had been published (Clement et al., 2012). In their study, the authors reported the results over five years (1997-2001) from a young (planting year = 1980-81) Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation located in Griffin Forest, central Scotland. Despite differing soil types, the partitioned fluxes from both our study and those from Griffin Forest indicated similar rates of R_{eco}, however, the longer growing season and higher carbon use efficiency at the coniferous forest resulted in higher rates (+48%) of NEE. At the time of publication, another, albeit relatively short-term (2007-2009), study reporting EC flux results from Wytham Woods, Oxfordshire had also recently been published (Thomas et al., 2011). As a mixed deciduous woodland in southern England, the Wytham study site was more comparable to our study site than Griffin Forest. However, despite similar rates of GPP at these two sites (Alice Holt and Wytham), substantially higher rates of R_{eco} at the Wytham site, resulted in a much lower mean annual NEE (130 g C m^{-2} yr^{-1}) compared to Alice Holt (486 g C m^{-2} yr^{-1}). In our paper we compared C flux figures from different sites (see Table 6) and we discussed the possible reasons for such large differences, including their contrasting management histories and differing lengths of observations. We suggested that less intensive forest management at the Wytham site (Kirby, 2010) over the past few decades may have resulted in more decomposing deadwood and possibly higher levels of heterotrophic respiration due to enhanced soil activity and C levels, therefore accounting for the higher levels of R_{eco} observed there.

The value to the scientific community of the knowledge, understanding and data sets developed for and through this publication is demonstrated by its citation in numerous subsequent studies and meta-analyses (e.g. Kimak and Leuenberger, 2015; Delpierre et al., 2016; Aubinet et al., 2018; Baldocchi et al., 2018). The data was used extensively by Heinemeyer et al. (2012) who investigated the relative contribution of different soil flux components to total soil CO_2 efflux. In this study, the authors demonstrated a significant temporal correlation between soil autotrophic respiration and canopy level GPP, indicating a fast mobilization of photosynthate, results that would not have been possible without simultaneous EC and soil flux data. The contribution that this paper has made within the discipline was exemplified by its inclusion in a recent review by Baldocchi et al. (2018). In this review paper, the authors used data from 59 long-term (defined as five or more years of

continuous measurements) EC sites from around the world to address key questions on the long-term variability in ecosystem carbon exchange and its partitioned fluxes. Consistent with our results, Baldocchi et al. (2018) showed that a disproportionate fraction of the yearly variability in NEE was associated with factors that influenced GPP rather than R_{eco}. In addition to contributing results and commentary from the only UK forest site, Baldocchi et al. (2018) specifically highlighted findings from our 2012 paper related to the impacts of defoliating insects on carbon fluxes. The importance and benefits of long-term study sites with Alice Holt quoted as an example were highlighted, the authors commented on their value in measuring short term disturbance events that may otherwise be missed. The authors also commented on the value of long-term EC measurements in general as they enable the separation of natural variability and emerging trends in ecosystem fluxes from sampling and measurement errors that may occur due to random noise or when half-hourly fluxes are summed to annual totals.

The results and concepts developed in Wilkinson et al. (2012) have also been presented at several major scientific conferences and workshops (see Appendix 1). This research has contributed to numerous site and educational visits, coordinated and hosted by the author, including a 2016 NERC post-graduate summer school. This work has also directly facilitated and contributed to numerous out-reach activities, including three award-winning art projects (e.g. Semiconductor, 2014). The scientific context and results have also been disseminated and presented on several TV programmes (e.g. BBC, 2017) and through online educational resources (e.g. Forest Research, 2017).

Forest management thinning, which removes targeted individual trees from a stand at intermediate stages of the forest growth cycle, is an important and commonly used silvicultural technique. In addition to providing some economic return prior to final felling in an even-aged rotation system, the removal of selected trees aims to improve the quality, yield and form of those that remain. Working at the same site as the previous paper, Wilkinson et al. (2016) used a combination of EC and aerial light detection and ranging (LiDAR) to improve understanding of the effects of thinning on forest carbon balance and canopy structure. At the time of publication there were only a few other studies that had investigated the impacts of management interventions on forest carbon balances using EC (e.g. Granier et al., 2008; Moreaux et al., 2011; Saunders et al., 2012; Vesala et al., 2005) with varying approaches used. In our study, the area and extent of the thinning operation was deliberately manipulated so that the EC tower was sited near the line dividing the thinned and un-thinned areas of the forest. Between June and August 2007, the eastern half of the study site (approx. 47.5 ha) was selectively thinned which resulted in a significant reduction in tree density (-37%) as well

as the addition of large quantities of woody debris to the forest floor. The western half of the

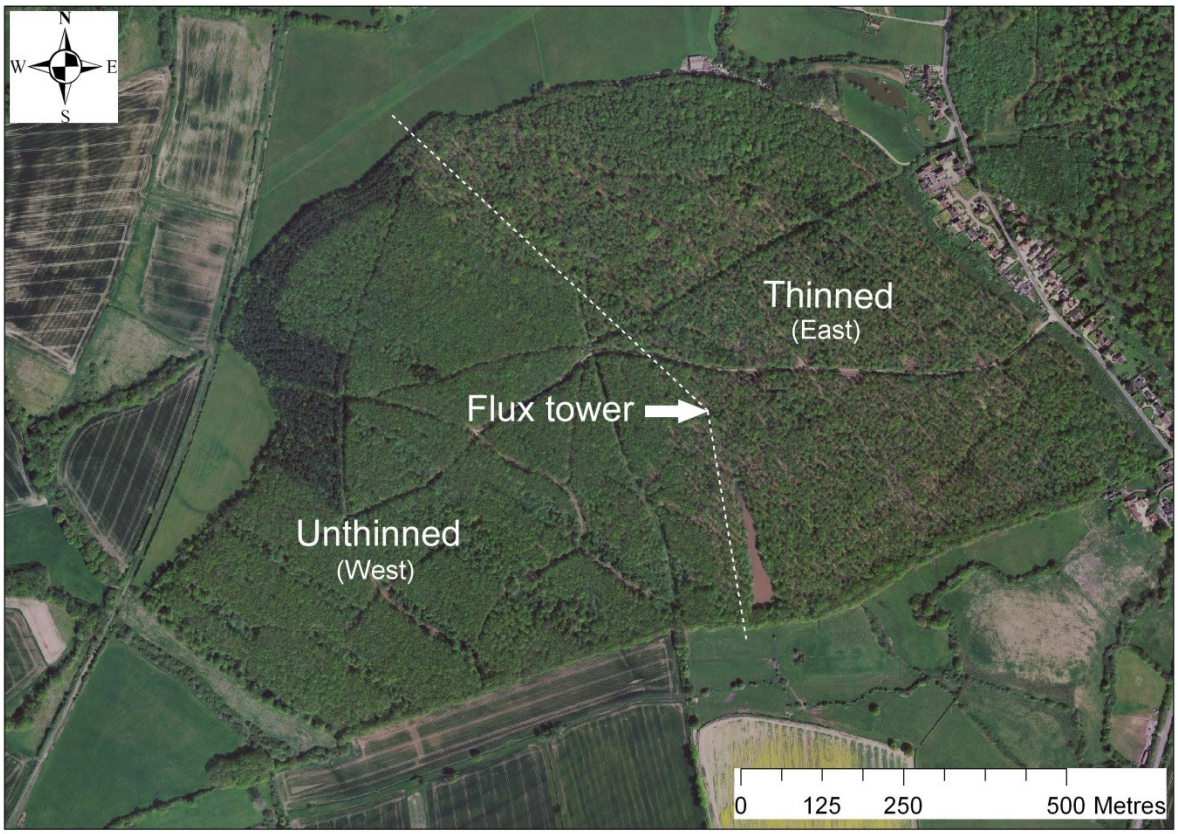

Figure 1. Aerial photograph (taken in spring 2008) of the Straits Inclosure, Alice Holt Forest. Bluesky International Ltd/Getmapping PLC.

forest was left un-thinned to act as a control area (Fig.1). Pre- and post-thinning LiDAR surveys indicated that thinning had a substantial impact on the forest canopy structure. The relative variability in canopy height (indicated by the coefficient of variation) increased substantially in the east but not in the west (see Table 4) as did the number of gaps in the forest canopy. The effects of thinning on the carbon fluxes were less evident. Contrary to our initial expectations, peak summer (June-August) maximum canopy photosynthetic rate in the first-year post thinning derived from light response curves, was unaffected. Ecosystem respiration fluxes increased in the thinned area relative to the un-thinned area in the post thinning phase, but not immediately. Our paper explored possible reasons for this and attributed this lack of photosynthetic response to better illumination of the ground vegetation and shrub layer, which we suggested was able to compensate for the removal of the upper tree canopy. We also suggested several factors that could account for the delayed increased in ecosystem respiration fluxes including; the break-down of woody debris following the thinning operation, soil disturbance due to machinery, local increases in temperature, increased throughfall, reductions in humidity and possible higher evaporation in the gaps.

Our findings of an apparent lack of response in peak photosynthetic capacity following management thinning were consistent with earlier studies that demonstrated how, as forest canopies become more structurally diverse, their light use efficiency can increase. This is thought to be related to a more even distribution of radiation throughout the canopy which improves the light penetration to sub-canopy species (Niinemets, 2007; Pangle et al., 2009). The paper has contributed to a number of empirical (Collalti et al., 2018; Lindroth et al., 2018) and modelling studies (Pinnington et al., 2017) that have continued to develop our understanding on impacts of forest management on forest carbon balances. Working at the same site, and basing their experimental design around our findings (thinned vs unthinned), Yamulki and Morison (2017) used a manual static chamber method to assess N_2O, CH_4 and CO_2 'forest floor' fluxes over 3-5 years. Although large woody debris was excluded in their chambers from the 'thinned area', their finding of higher respiratory CO_2 fluxes from areas of the forest that were the most recently thinned was consistent with our EC paper. The evidence (CO_2 fluxes) and ideas (compensatory photosynthesis) from our paper have been cited in a number of other studies related to post thinning changes in the balance between autotrophic and heterotrophic respiration (Mazza et al., 2019) and changes in understorey fluxes (Teramoto et al., 2017). The results and ideas that were developed through this publication have also been presented at several international scientific workshops and conferences (see Appendix 1).

Vegetation phenology, which is the timing of seasonal developmental stages in plant life cycles (Kimball, 2014) is a key regulator of both ecosystem processes and biosphere feedback to the climate system (Richardson et al., 2018). Phenological responses have been shown to be sensitive indicators of the impacts of climate change on the biosphere; for example, advances in the date of spring budburst over recent decades have been widely observed across a range of plant species (Settele et al., 2014). An average advance in spring/summer development of 2.5 days decade $^{-1}$ was reported by Menzel et al. (2006) for a range of plant species across Europe. The impacts of changes in phenology may have serious consequences for natural and managed ecosystems, for example resulting in ecosystem trophic mis-match (Thackeray et al., 2010). Such changes could also have important implications for carbon and water balances of forest, where earlier budburst could potentially lead to longer growing seasons, or increased frost risk. Changes in forest phenology will also have important impacts on how we plan and manage our future forests and will need to be taken into account when choosing species and provenances to be planted. The next two papers presented in this thesis focused on developing understanding of forest phenology by assessing: a) the impacts of recent inter-annual variation in climate on tree phenology of different provenances (Wilkinson et al., 2017) and, b) the development of a low-cost, non-destructive approach to enhance phenological measurements in forest ecosystems (Wilkinson, et al., 2018).

With ambitious future targets to plant 11 million new trees set by the UK government (DEFRA, 2018) and calls by the UK CCC for forest cover to be increased from 13% to 17% by 2050 (UK CCC, 2019) planting of both novel species and different provenances of native species is of considerable interest to the forestry sector. The practise of planting southern material has been widely used in UK forestry due to evidence of improved early vigour (Whittet et al., 2019). Provenances that have been sourced from more southerly locations should also be better suited to future climatic conditions however, the scientific understanding and basis for this is based on a very limited number of European wide provenance trials and has tended to focus on assessing tree suitability, form and productivity. Wilkinson et al. (2017) assessed variations in the timing of budburst across 23 different European provenances of oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) over an eight-year period at a provenance trial in the south of England. Temporal trends in the date of budburst were identified using a combination of general linear models and three-dimensional temperature response surfaces. This study demonstrated that the order in which the different provenances reached budburst was consistently related to their source latitude; the southern provenances were always earlier than those from more northerly latitudes. The study also demonstrated that the southern provenances were more frequently exposed to potentially damaging low air temperatures during late spring. Our findings of a clear latitudinal cline for spring phenology in oak trees were consistent with the results from other common garden trials (e.g. Kleinschmit, 1993; Deans and Harvey, 1996). The timing of spring phenology such as budburst and leaf unfolding in a majority of temperate plants is associated with two distinct temperature-driven processes. Following leaf fall in autumn, a period of cold temperature during which chilling is accumulated is required for the completion of endodormancy; this is followed by a period of warming required for bud and subsequently leaf development. Using PLS, our study identified, for each provenance, when these periods of chilling and warming are likely to occur. The study demonstrated that spring warming had a larger effect on budburst than winter chilling with a mean spring temperature-driven advance of 3.61 days/°C (standard error = 0.17 days/°C). We acknowledged in this paper that this estimate, which although consistent with those from other similar studies (e.g Morin et al., 2010; Fu et al., 2013) is too low to account for the advance in budburst in temperate tree observed over recent decades. In this paper we discussed possible reasons for this mismatch, including different approaches when deciding the appropriate spring warming period to use and possible non-linear temperature responses. This paper has contributed to scientific studies on both the future of native woodland under climate change (Esplugas, 2018) and to a spatial analysis of leaf phenological responses (Guada et al., 2019). The paper has also been used to support evidence for developing FC policy around the use and planting of native tree provenances (J.Weir, personal communication, April 18, 2019; Whittet et al., 2019).

The final publication continued the theme of forest phenology research through the development of a low-cost, non-destructive improvement to phenology measurements in forests. Over the past ten years, there have been a number of studies published that have used different camera systems to study phenological development patterns across a wide range of ecosystems (e.g. Sonnentag et al., 2012; Wingate et al., 2015; Moore et al., 2017). This growing body of evidence is making a valuable addition to alternative approaches of monitoring vegetation phenology such as satellite remote sensing (e.g. White et al., 2014), experimental warming (e.g. Wolkovich et al., 2012), long-term observations from phenological garden networks (e.g. Menzel et al., 2006) or the use of citizen science observers e.g. woodland trust nature calendar (https://naturescalendar.woodlandtrust.org.uk/). Whilst remote sensed phenology data can suffer from poor temporal and spatial resolution especially when viewing highly heterogeneous ecosystems such as forest canopies, manual phenological measurements, recorded by observers in the field, are labour-intensive and can suffer from subjective interpretation. For specific phenological indicators associated with forests, budburst, leaf expansion or senescence the use of automated techniques such as repeat digital photography of a known area of forest canopy is a useful alternative that addresses some of these issues. It is not surprising therefore that its use has increased across a range of different ecosystems at monitoring sites around the world over recent years (e.g. Wingate et al., 2015; Nagai et al., 2018; Richardson et al., 2018) and that standardized systems and operational protocols have been developed in order to harmonize this near-remote sensing approach (e.g. Hufkens et al., 2018). In forests these 'phenocam' systems are generally mounted on tall towers or masts to provide appropriate top-down views of forest canopies. However, such towers are logistically difficult to install and are expensive. To address this problem, Wilkinson et al. (2018) investigated whether a ground-based camera system (pointing upwards) could provide a suitable alternative to tower mounted systems (pointing downwards). This study compared images from a pair of identical cameras, one ground-based, and one tower-based, viewing the same trees at the Alice Holt deciduous oak forest. Building on analysis techniques developed with T.Mizunuma a PhD student who worked at Alice Holt (see Appendix 1), the timing of key phenological events were identified. The onset of spring green-up and canopy senescence were extracted from colour indices derived from the digital images using piecewise regression analysis for both cameras systems. Over the six years (2011-2016) that this study took place, spring green-up from the tower-based system ranged from day 108-126. Despite variation between years, the upward-facing camera system was able to detect key spring phenological events to the same extent as the more usual downward-facing camera (mean difference of two days for the spring green-up date). However, the upward- and downward-facing systems were less well-matched in detecting specific events at the end of the growing season (mean difference of eighteen days for onset

of senescence). In this paper, we discussed possible reasons for this lack of agreement at the end of the growing season such as: differing illumination conditions, differing views of the camera systems and the impacts of missing data when images had been rejected due to rain, fog or fallen leaves during autumn. In addition to the phenological information derived from the analysis of colour signals, this study also demonstrated that upward-facing camera systems can usefully provide further information about the structural dynamics of a broadleaved forest. The greater ease and lower cost with which ground-based systems can be deployed could allow data collection over a wide area with multiple cameras which offers a clear advantage in heterogeneous forest light environments.

One of the very few other studies that has also compared the results from upward and downward facing cameras, albeit over a shorter time period than ours, in this case three growing seasons (compared to our study based on six), was that of Nagai et al. (2013). This study used images from a deciduous broadleaved forest and an evergreen coniferous forest in Japan. Consistent with our study, the authors demonstrated a good agreement between the phenology measured by a pair of upward- and downward-facing cameras in detecting spring events at the broadleaved forest. The upward images failed to capture the canopy level phenology at the evergreen coniferous forest site which the authors suggested was due to both canopy architecture and the spectral characteristics of the conifer canopy.

Due to its relatively recent publication, it is difficult to assess the contribution that Wilkinson et al. (2018) has had or will have on future studies. We successfully demonstrated that ground-based systems can provide a viable alternative to tower-based camera systems, at least in deciduous forests. As ground-based upward-facing camera systems do not require the same extensive infrastructure required by tower-based downward-facing systems and do not have the problems inherent with their installation, maintenance and use, they are much more suitable for widespread deployment for forest monitoring. Whether this is taken up at other monitoring sites or by other research groups, remains to be seen. However, this is a developing area and current trends suggest that a future network of sites (e.g. as developed for EC through Fluxnet) would enhance our understand of global phenology, if so, this work would help in developing possible approaches. Further testing of this approach is ongoing at Alice Holt. Four extra upward facing cameras were installed in 2018, additional canopy parameters such as litterfall and radiation interception (model LAI-2200C, LI-COR Biosciences, Lincoln, Nebraska, USA) are also being measured regularly at these four camera locations. Further technical developments of this approach and the creation of a long-term data sets of camera-based phenology with increased spatial representation will continue to help inform our understanding on the links between climate, phenology and carbon fluxes.

Chapter 7 - Synthesis of knowledge gained and future direction for research

7.1 Outline

The purpose of this chapter is to synthesise the knowledge gained, and the original ideas developed, through the publications presented in this thesis. The chapter is structured around specific themes related to temperate forest/climate interactions that have emerged over the course of this research. Gaps in our current knowledge identified in the publications, and the 'lessons learnt', are also discussed. The chapter concludes with a series of specific recommendations for future research.

7.2 Effects of disturbances on forest carbon balances

One of the themes central to several publications in this thesis is understanding the causes of inter-annual variation in carbon exchange at an oak woodland in the south of England. Some of this variation has been directly attributed to environmental factors such as low soil moisture, which was shown to reduce the responsivity of R_{eco} to air temperature (Wilkinson et al., 2012). Additionally, forest disturbance also emerged as a key theme linking the different studies. A range of different disturbances such as canopy defoliation by insects, disease, late spring frost events and forest management interventions were all observed and investigated and emerged as another important cause of inter-annual variation in carbon fluxes.

Developing the understanding of how land-atmosphere interactions and GHG emissions reporting may be influenced by forest management is important, especially given current government targets in England (DEFRA, 2018) to bring large areas of under-managed woodland back into sustainable management. As part of this thesis, two studies (Wilkinson et al., 2016; Pinnington et al., 2017) investigated the impacts of forest management on the carbon dynamics of the Straits Inclosure oak woodland. Whilst the first of these studies focused on assessing the impacts of thinning carried out in the eastern half of the forest block in 2007, the second was based on the thinning in the western half, completed in 2013. Although these two thinning events were carried out in different areas of the forest and under different meteorological conditions, they both occurred within the EC footprint and on the same soil type. These two independent events therefore provided a valuable opportunity to quantify the impacts of disturbances through forest management on forest carbon dynamics. The results from both studies were largely in agreement; both demonstrated a surprising lack of response by NEE to each thinning, the NEE measured from thinned areas relative to un-thinned areas did not change substantially in the first three years post thinning. Wilkinson et al. (2016) hypothesised that this lack of response was due to a compensatory increase in NEE by ground vegetation and shrub layer species that, prior to the management, may have been light limited. However, in Pinnington et al. (2017), that I co-authored, new evidence from

process modelling enabled a revision to this interpretation. In this second study, the 2013 thinning event was modelled using a Data Assimilation Linked Ecosystem Carbon (DALEC2) model (Bloom & Williams, 2015). The overall results were similar to the earlier study, but in Pinnington et al. (2017) we demonstrated that the apparent lack of response in NEE during the post-thinning phase was due to a reduction in GPP, following a decrease in total leaf area, and that the reduction in GPP was offset by a simultaneous reduction in R_{eco}. The use of numerical data assimilation techniques embedded within ecosystem carbon dynamics models is clearly a powerful tool and, in this case, resulted in new insights into the forest functioning that previously were not possible. For example, in Wilkinson et al. (2015) we attempted to partition and gap-fill the separated EC data for the thinned and un-thinned areas of the forest, before and after the 2007 thinning, using the empirical modelling method proposed by Reichstein et al. (2005). However, the use of this gap-filling and partitioning approach, with thinned and un-thinned areas of the forest segregated by wind direction, drew strong criticism from the Journal's reviewers. They argued that our annual gap-filled partitioned fluxes for each sector of the forest were likely to contain unacceptably large uncertainties, due to low amounts of original data (27.7% and 35.9% original quality-controlled data availability for the thinned and un-thinned sectors respectively). We accepted that their criticism was justified and, in our final revised manuscript (Wilkinson et al., 2016) changed our approach to focus on process responses based on averaged non filled data rather than calculating seasonal or annual sums. In retrospect, more systematic mensuration and biometric measurements, especially of the different understorey components and in different areas of the forest would have provided valuable ground-based data to substantiate the ideas developed in Wilkinson et al. (2016). Furthermore, detailed measurements of below ground carbon allocation (e.g. soil carbon, roots and root exudates) in different parts of the forest would also have been valuable in helping to explain differences between the two treatments.

Over the course of this research, natural forest disturbance events have also occurred and been measured at the study site. Wilkinson et al. (2012) reported the impacts of severe outbreaks of defoliating moth caterpillars, mostly *Tortrix viridana* L. and *Operophtera brumata* L. that caused considerable damage to the forest canopy in 2009 and 2010. The increased insect activity in those years also resulted in additional nitrogen deposition to the forest floor (Benham et al., 2012). In addition, there are likely to have been some effects of the oak powdery mildew (*Erysiphe alphitoides*) which infected a number of oak trees during the same years. In that 2012 paper, we hypothesised that low annual sums of GPP in these two years were due to the reduced canopy area. However, because of the method by which these fluxes are calculated (Reichstein et al., 2005) we did not explicitly explore the link between GPP and R_{eco}. Using EC, GPP is not a measurable parameter, but is calculated as the sum of NEE (measured) and R_{eco} (modelled), therefore, GPP and R_{eco} are not independent measurements

(Baldocchi & Sturtevant, 2015). In retrospect, an alternative and possibly stronger approach to the one presented in Wilkinson et al. (2012) would have been to model the partitioned carbon fluxes in the absence of caterpillars or disease outbreaks and then to compare the results with the actual measurements during the affected years. In the future, the process modelling approach and findings presented in Pinnington et al. (2017) could be used for a re-analysis of the data presented in Wilkinson et al. (2012), updated with more recent years of CO_2 flux data. A study of this type would help to develop further understanding on the response of forest R_{eco} and GPP to disturbance events, such as following the outbreak of defoliating insects.

7.3 Linking phenology and forest carbon balances

In forests, canopy structure and phenology have a key role in the global carbon cycle because biological land surface characteristics affect how energy, water and GHGs are exchanged with the atmosphere. Furthermore, where long-term trends in phenology are observed, this may act as a natural indicator of human induced climate change (UK CCC, 2017). The link between changes in the timing of key biological events and forest carbon dynamics has also emerged as a key theme in this thesis.

The relationship between seasonal changes in canopy colour (derived from repeat digital photography) and ecosystem carbon fluxes was investigated in a paper that I co-authored (Mizunuma et al., 2013). In addition to providing a permanent visual record that can be inspected to determine the phenological state of vegetation, quantitative data on the colour of the vegetation can also be extracted from the raw images to provide a proxy for phenological state. In this study, we showed that the timing of spring increase and autumn decline in GPP approximately followed the seasonal pattern in canopy colour derived indices (e.g. S_{green} and Hue). A late air frost on the 12th May, 2010 was also detected in both the Hue and S_{green} colour signals from the camera systems which resulted in a slight reduction to daily accumulated GPP. This paper added to the growing body of literature that has demonstrated the usefulness of archived canopy images in monitoring forest canopy condition and physiology.

A longer term phenology study that quantified inter-annual fluctuation in the date of budburst across a range of European oak provenances was published in Wilkinson et al. (2017). In this study, observations included a provenance of oak sourced from the local area (Chiddingfold, Surrey). Over the course of eight years, the timing of spring budburst in this local provenance was very close to the timing of budburst detected in the camera systems at the nearby Alice Holt flux site. The existence of a strong relationship between manually observed budburst in the local oak provenance and the onset of a green up signal detected from canopy images enabled further research. Using results that were published in Wilkinson et al. (2017) the impacts of altered growing season length were investigated in a poster presentation

'*Implications of altered phenology on the carbon dynamics of deciduous oak woodland*' that I presented at the 2016 EGU conference (Wilkinson et al., 2016b). In this study, the NEE observations and camera-derived day of budburst were assimilated into DALEC2. A series of experiments were run with the model using these parameter sets, but altering the timing of budburst (-10, -5, +5, +10 days) to reflect the variation observed across a range of European provenances at the Chiddingfold phenology trial. The earliest budburst scenario (-10 days) increased mean annual NEE by 14%, supporting the evidence that earlier budburst could result in enhanced carbon uptake. Over a 5-year period, earlier budburst (-10 days) resulted in an extra 274 gC m^{-2} yr^{-1} sequestration compared to model predictions using the mean observed date. In this poster presentation (Wilkinson et al., 2016b), we acknowledge that this modelling method may be an over simplification because it is focused solely on differences at the start of the growing season. Whilst earlier budburst may result in an earlier onset of the growing season (and, therefore, the carbon uptake period), its total length is a function of the timing of both spring and autumn. The timing and impacts of changes in 'end of season' phenology, and therefore changes in the carbon uptake period on annual NEE budgets was investigated for a conference presentation (Wilkinson et al., 2016c). However, despite using a proven methodology (Fu et al., 2017) clear conclusions could not be drawn. This may be because disturbance events (section 7.2) have a larger effect on seasonal carbon uptake than more subtle effects resulting from small changes to growing season length. This remains a subject area that is under researched and represents a gap in knowledge that should be the focus of future research.

7.4 Research recommendations

The following section highlights future research questions that have developed over the course of this thesis and that warrant further investigation.

1. *Improved quantification and understanding of EC partitioned fluxes.*

Across the UK, extreme climatic events such as heatwaves and droughts are becoming more frequent (UKCP18) and forests are repeatedly exposed to an ever-wider range of environmental conditions. To better understand the impacts of these extreme climatic events on forest carbon balances, accurate measurements of partitioned CO_2 fluxes, NEE, GPP and R_{eco} are required. However, as previously discussed (see section 7.2) assessing ecosystem level GPP and R_{eco} from measurements of NEE is complicated by the fact that GPP cannot be measured directly using EC, it can only be estimated using flux partitioning methods. The most common method used by the EC community, developed by Reichstein et al. (2005) involves modelling R_{eco} as a function of either soil or air temperature using night-time data and extrapolating these relationships to day-time conditions. Alternatively, R_{eco} can be estimated by extrapolating the response curve between canopy level photosynthesis and light to its zero

intercept (Xu & Baldocchi, 2004). Concern about both these approaches has centred around the 'closure problem' whereby two pieces of information are derived from one equation (Baldocchi & Sturtevant, 2015), in this case GPP and R_{eco} both contain information about NEE which may result in spurious correlations between all three variables. As a direct signal from plant photosynthetic systems, sun-induced chlorophyll fluorescence (SIF) has the potential to provide additional and detailed information related to canopy photosynthetic and physiological dynamics, potentially acting as a tracer for GPP (Gu et al., 2019). The increasing availability of field deployable spectrometers is opening up the possibility of long-term SIF measurements at the forest canopy level. Future research will therefore aim to investigate the potential for combined EC observations with canopy level and drone-based SIF measurements at our deciduous oak flux site. The expected outcomes for this work will be a better understanding of forest GPP and how this links to other canopy scale processes and environmental conditions such as droughts. Ultimately, this should lead to an improved quantification of forest carbon dynamics and support the development of models to estimate GPP at regional to continental scales (e.g. Ogutu et al., 2013).

2. *Assessing intra-forest variation in phenology and canopy dynamics using networks of low cost sensors.*

The timing and extent of forest canopy development is important in regulating forest/atmosphere interaction such as CO_2 and energy exchange, canopy water interception and canopy evapotranspiration rates. However, the spatial and temporal variation in forest canopy attributes such as LAI and canopy gap fraction is often large and poorly represented in field scale measurements. Forests with spatially diverse and complex understorey layers, commonly found in managed deciduous forests present an even greater measurement challenge. A variety of techniques including: manual hemispherical photography (Evans & Coombe, 1959), terrestrial laser scanning (TLS) (Disney, 2019), aerial LiDAR (García et al., 2018) and light interception have all been used to quantify forest canopy structure. However, none of these approaches are suitable for high frequency long-term measurements at scales consistent with EC footprints results. Future research will therefore investigate extending the use of multiple networked RaspberryPi camera systems to improve the spatial sampling of forest canopy dynamics. In addition, high frequency images, typically every 30 minutes during daylight hours (to record changes with illumination angle) and from multiple heights within the forest canopy will enable a separation of understorey and upper canopy dynamics. This approach is already being tested at the Alice Holt flux site where four upward facing cameras (Fig.2) have been fixed to existing litterfall traps. Canopy parameters such LAI and canopy gap fraction are being derived from high frequency images using the open sourced canopy analysis package CIMES-FISHEYE (Gonsamo et al., 2011). These results are being tested

against other established measurements, for example canopy structural parameters are also being measured at the same locations using a LAI-2200C Plant Canopy Analyzer (LI-COR Inc., Lincoln, NE USA).

Figure 2. (a) Example canopy image taken on 13th January 2019 using a networked RaspberryPi camera board and 'fish eye' 170° lens (b) RaspberryPi camera system and enclosure at the the Straits Inclosure, Alice Holt Forest.

The expected outcomes of this research will be the further development of a system offering improved spatial and temporal resolution of forest canopy monitoring that is suitable for long-term measurements and at a reasonable cost.

3. *Assessing long-term trends in forest Water Use Efficiency (WUE) using EC forest flux measurements*

The global atmospheric CO_2 concentration ($[CO_2]$) has been increasing over the last two decades at a rate 2 ppm y^{-1} (Francey et al., 2013). Increases in water-use efficiency (WUE), the ratio of carbon assimilation to water loss across a range of temperate and boreal forests in the Northern Hemisphere have been shown to be strongly linked to $[CO_2]$ and, long-term trends in WUE are emerging (Keenan et al., 2013). Previous studies where UK forest sites have been included in wider European forest networks (e.g. Saurer et al., 2014; Frank et al., 2015) have focused on tree-ring carbon isotope measurements to determine WUE and so far only a limited number of species have been measured. GPP and evapotranspiration derived from EC data can also be used to measure stand scale WUE. Where EC data are used for this type of analysis, it is necessary to account for the effects of atmospheric evaporative demand and therefore 'inherent' WUE (IWUE) is normally calculated. IWUE represents the ratio of GPP to stomatal conductance. EC measurements of carbon dioxide, water vapour and energy fluxes commenced at Alice Holt in 1998 and have continued to the present. Most of

the studies and publications resulting from this long-term EC record have focussed on answering questions related to different aspects of the carbon cycle. The long-term Straits record is therefore an opportunity to assess the effects of increasing atmospheric [CO_2] on the IWUE of an oak forest in southern England. The expected outcomes from this research will be a better understanding of the links between UK broadleaved forests and the hydrological cycle under conditions of rising atmospheric [CO_2].

7.5 Conclusion

Through their ability to remove CO_2 from the atmosphere, forests play a key role in helping international attempts to limit GHG concentrations aimed at stabilizing human induced climate change (Bastin et al., 2019). However, interactions between forests and the atmosphere are complex and large uncertainties still remain in many of these processes. This thesis highlights multiple aspects related to temperate forest functioning in a changing climate and represents a small contribution to the scientific understanding and evidence base in this subject area. Research into the inter-annual variability on the carbon balance, the effects of management and the phenology of an oak woodland growing in the south of England have been presented and discussed.

Innovations in measurement techniques, instrumentation and data science will continue to develop in this diverse field over future years. The integration of existing long-term data sets with new measurements and innovative data science will provide new insights and understanding within this complex field.

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Appendix 1 - Other published work related to forest/climate interactions

Comments in red italics indicate the contribution by M.Wilkinson.

Scientific Publications

Büker, P., Feng, Z., Udding, J., Briolat, A., Alonso, R., Braun, S., Elvira, S., Geroes, G., Karlsson, P.E., Le Thiec, D., Marzuoli, R., Mills, G., Oksanen, E., Wieser, G., **Wilkinson, M.** and Emberson, L.D. (2015). New flux based dose response relationships for ozone for European forest treee species. Environmental Pollution 206:163-174. *M.W. carried out measurements, supplied data and commented on the final manuscript.*

D'Odorico, P., Gonsamo, A., Gough, C.M., Bohrer, G., Morison, J., **Wilkinson, M.**, Hanson, P.J., Gianelle, D., Fuentes, J.D. and Buchmann, N. (2015). The match and mismatch between photosynthesis and land surface phenology of deciduous forests. Agricultural and Forest Meteorology 214-15: 25-38. *M.W. carried out measurements, supplied data and commented on the final manuscript.*

Heinemeyer, A., **Wilkinson, M.**, Vargas, R., Subke, J.-A., Casella, E., Morison J.I.L. and Ineson, P. (2012). Exploring the "overflow tap" theory: linking forest soil CO_2 fluxes and individual mycorrhizosphere components to photosynthesis. Biogeosciences 9: 79–95. *MW supervised the measurements, supplied data, contributed to theory development, discussed the results and contributed to the final manuscript.*

Ilie, I., Dittrich, P., Carvalhais, N., Jung, M., Heinemeyer, A., Migliavacca, M., Morison, J.I.L, Sippel, S., Subke, J.-A., **Wilkinson, M.**, and Mahecha, M.D. (2016). Reverse engineering model structures for soil and ecosystem respiration: the potential of gene expression programming. Geoscientific Model Development Discussions. doi:10.5194/gmd-2016-242. *M.W. carried out measurements and supplied data.*

Mizunuma, T., **Wilkinson, M.**, Eaton, E.L., Mencuccini, M., Morison, J.I.L., and Grace, J (2013). The relationship between carbon dioxide uptake and canopy colour from two camera systems in a deciduous forest in southern England. Functional Ecology, 27(1). doi: 10.1111/1365-2435.12026. *MW helped supervise the project, carried out measurements, supplied data, contributed to theory development and contributed to the final manuscript.*

Moffat, A.J., Benham, S., Morison, J.I.L., Pitman, R., Vanguelova, E.I., **Wilkinson, M.** and Yamulki, S. (2010). The value of forest monitoring in developing forest ecosystem science in Britain. In: John Derome – Ambassador for forest monitoring in Europe, L. Ukonmaanaho, K. Derome, P. Rautio and P. Merilä (eds), Working Papers of the Finnish Forest Research Institute 180, Helsinki. *M.W. carried out measurements, supplied data and contributed to the final manuscript.*

Musavi, T., Migliavacca, M., van de Weg, M.J., Kattge, J., Wohlfahrt, G., van Bodegom, P.M., Reichstein, M., Bahn, M., Carrara, A., Domingues, T.F., Gavazzi, M., Gianelle, D., Gimeno, C., Granier, A., Gruening, C., Havránková, K., Herbst, M., Hrynkiw, C., Kalhori, A., Kaminski, T., Klumpp, K., Kolari, P., Longdoz, B., Minerbi, S., Montagnani, L., Moors, E., Oechel, W.C., Reich, P.B., Rohatyn, S., Rossi, A., Rotenberg, E., Varlagin, A., **Wilkinson, M**., Wirth, C., and Mahecha, M.D. (2016). Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits. Ecology and Evolutionprimary productivity by plant phenology and physiology. Proceedings of the National Academy of Sciences of the United States of America. Vol 12 no. 9: 2788-2792. doi:10.1073/pnas.1413090112. *M.W. carried out measurements and supplied data.*

Nagai, S., Akitsu, T., Saitoh, T.M. et al. **(inc Wilkinson, M.)** (2018). 8 million phenological and sky images from 29 ecosystems from the Arctic to the tropics: the Phenological Eyes Network. Ecological Research 33: 1091-1092. *M.W. carried out measurements, supplied data and contributed to the final manuscript.*

Pinnington, E.M., Casella, E., Dance, S.L., Lawless, A. S., Morison, J.I.L., Nichols, N.K., **Wilkinson, M.** and Quaife, T.L. (2016). Investigating the role of prior and observation error correlations in improving a model forecast for forest carbon balance using Four-dimensional Variational data assimilation. Agricultural and Forest Meteorology 228: 299-314. doi:10.1016/j.agrformet.2016.07.006. *MW helped supervise the project, carried out measurements, supplied data and commented on the final manuscript.*

Pinnington, E.M., Casella, E., Dance, S.L., Lawless, A. S., Morison, J.I.L., Nichols, N.K., **Wilkinson, M.** and Quaife, T.L. (2017) Understanding the effect of disturbance from selective felling on the carbon dynamics of a managed woodland by combining observations with model predictions. Journal of Geophysical Research: Biogeosciences, 122(4), pp. 886–902. doi: 10.1002/2017JG003760. *MW helped supervise the project, carried out measurements, supplied data, contributed to theory development and contributed to the final manuscript.*

Ward, H.C., Kotthaus, S., Grimmond, C.S.B., Bjorkegren, A., **Wilkinson, M.**, Morrison, W.T.J., Evans, J.G., Morison, J.I.L. and Iamarino, M. (2014). Effects of urban density on carbon dioxide exchanges: observations of dense urban, suburban and woodland areas of southern England. Environmental Pollution 198: 186-200. doi: 10.1016/j.envpol.2014.12.031 *M.W. carried out measurements, supplied data and contributed to the final manuscript.*

Wingate, L., Ogeé, J., Cremonese, E., Filippa, G., Mizunuma, T. et al. **(inc Wilkinson, M.)** (2015) 'Interpreting canopy development and physiology using a European phenology camera network at flux sites', *Biogeosciences*, 12(20). doi: 10.5194/bg-12-5995-2015. *M.W. carried out measurements, supplied data and contributed to the final manuscript.*

Book Chapters

Vilhar, U., Beuker, E., Mizunuma, T., Skudnik, M., Lebourgeois, F., Soudani K. and **Wilkinson, M**. (2013). Measurement methods for above-ground vegetation - Tree Phenology. In: Ferretti, M. and Fischer, R. (eds). Forest Monitoring. Scientific methods for the terrestrial monitoring of temperate and boreal forests. Elsevier, Amsterdam, pp. 169-182. *M.W. carried out measurements, supplied data and contributed to writing the chapter.*

Scientific conference and workshop posters

Wilkinson, M., Eaton. E.L., Casella, C., Crow, P., and Morison, J.I.L. (2013). Effects of management thinning on carbon dioxide uptake by a plantation oak woodland in SE England. European Geosciences Union General Assesmbly, Vienna 12th-17th April 2013. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted the poster and the designed the figures. Co-authors discussed the results and commented on the final manuscript.*

Wilkinson, M., Eaton, E.L., Pinnington, E.M. and Morison, J.I.L. (2016). Implications of altered phenology on the carbon dynamics of deciduous oak woodland. European Geosciences Union General Assesmbly, Vienna 12th-17th April 2016. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted the poster and the designed the figures. Co-authors discussed the results and commented on the final manuscript.*

Wilkinson, M., Eaton, E.L. and Morison J.I.L. (2017). How does tree seed provenance affect budburst date for oaks in southern England? South Downs National Park Research Conference, Midhurst, 6th July 2017. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted the poster and the designed the figures. Co-authors discussed the results and commented on the final manuscript.*

Xenakis,G., **Wilkinson, M**., Perks, M. and Morison, J.I.L. (2019). The impact of the 2018 drought on carbon capture of two major UK forest types. 1st Climate Change Forum of the RMetSoc, London, 4th June 2019. *MW helped developed the original idea, carried out some of the measurements, performed some data analysis, helped draft the poster and designed some figures. Co-authors also helped draft the poster, discussed the results and commented on the final design.*

Scientific conference and workshop oral presentations

M. Wilkinson, E. Casella, P. Crow, J. Morison. Effects of management thinning on CO_2 uptake by a plantation oak woodland in SE England. CarboForest Conference, Polish Forest Research Institute, Warsaw, Poland, 21-23 September 2011. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted and delivered the presentation. Co-authors commented on the presentation.*

Wilkinson, M and Eaton, E.L. Linking forest carbon fluxes and phenology in the South Downs National Park. South Downs National Park Research Conference, Midhurst, 6th July 2015. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted and delivered the presentation. Co-authors commented on the presentation.*

M. Wilkinson, S.E. Benham, E.L. Eaton, E.M. Pinnigton & J.I.L. Long-Term Trends in Carbon Dynamics and Spring Phenology at Alice Holt Research Forest. 2nd ICOS Science Conference, Helsinki, Finland 27-29 September 2016. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted and delivered the presentation. Co-authors commented on the presentation.*

M. Wilkinson, E.L.Eaton, J. Morison, E. Vanguelova and G. Xenakis. The role of soil carbon fluxes in the measurement and management of forest carbon balances: current perspectives and future challenges. Royal Society Discussion meeting on 'Soil-atmosphere carbon fluxes - experimentalists meet modellers', Kalvi Royal Society Conference Centre, Buckinghamshire, 12 - 13th October 2017. *MW developed the original idea, carried out the measurements, performed the data analysis, drafted and delivered the presentation.*

Videos and online resources

Forest Research (2017) *Measuring the carbon and greenhouse gas balance of a UK woodand*. Available at: https://vimeo.com/223136163 (Accessed: 12 July 2019). *MW drafted the text and delivered the interview.*

Semiconductor (2014). Available at: https://semiconductorfilms.com/art/cosmos/ (Accessed: 12 July 2019). MW drafted some text and delivered the interview.

Appendix 2 – FORM UPR16 Research Ethics Review Checklist

FORM UPR16

Research Ethics Review Checklist

Please include this completed form as an appendix to your thesis (see the Research Degrees Operational Handbook for more information

Postgraduate Research Student (PGRS) Information				Student ID:	911840
PGRS Name:	Matthew Wilkinson				
Department:	Biological Sciences	First Supervisor:	Dr Mat Tallis		
Start Date: (or progression date for Prof Doc students)	1st October 2018				
Study Mode and Route:	Part-time ☒	MPhil ☐	MD ☐		
	Full-time ☐	PhD ☒	Professional Doctorate ☐		

Title of Thesis:	The carbon dynamics and phenology of oak woodland growing in south-east England
Thesis Word Count: (excluding ancillary data)	8268

If you are unsure about any of the following, please contact the local representative on your Faculty Ethics Committee for advice. Please note that it is your responsibility to follow the University's Ethics Policy and any relevant University, academic or professional guidelines in the conduct of your study

Although the Ethics Committee may have given your study a favourable opinion, the final responsibility for the ethical conduct of this work lies with the researcher(s).

UKRIO Finished Research Checklist:
(If you would like to know more about the checklist, please see your Faculty or Departmental Ethics Committee rep or see the online version of the full checklist at: http://www.ukrio.org/what-we-do/code-of-practice-for-research/)

a) Have all of your research and findings been reported accurately, honestly and within a reasonable time frame?	YES ☒ NO ☐
b) Have all contributions to knowledge been acknowledged?	YES ☒ NO ☐
c) Have you complied with all agreements relating to intellectual property, publication and authorship?	YES ☒ NO ☐
d) Has your research data been retained in a secure and accessible form and will it remain so for the required duration?	YES ☒ NO ☐
e) Does your research comply with all legal, ethical, and contractual requirements?	YES ☒ NO ☐

Candidate Statement:

I have considered the ethical dimensions of the above named research project, and have successfully obtained the necessary ethical approval(s)

Ethical review number(s) from Faculty Ethics Committee (or from NRES/SCREC):	

If you have *not* submitted your work for ethical review, and/or you have answered 'No' to one or more of questions a) to e), please explain below why this is so:

This PhD thesis by prior publication is a retrospective analysis of my previously published scientific papers. This work was entirely funded by my employer, the Forestry Commission and all internal and government procedures related to publishing in the public domain were followed, including those covered by 'Crown Copyright'. Prior to publication all of the research discussed had undergone rigorous internal and external peer review.

Signed *(PGRS)*:		**Date:** 03/09/2019